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VOL. XXXIX] LAWRENCE, NOVEMBER 18, 1958 [NO. 1

Additions to the Known Herpetological Fauna of Costa Rica with Comments on Other Species. No. III.

BY

EDWARD H. TAYLOR

ABSTRACT: This paper treats of a series of Costa Rican Salientia. Two species, *Hyla microcephala microcephala* Cope and *Eleutherodactylus monnichorum* Dunn, are reported from Costa Rica for the first time. The following species are described as new: *Dendrobates granuliferus, Eleutherodactylus taurus, Hyla legleri* and *Hyla dulcensis*. The species *Hyla monticola Cope*, long known only from the type specimen (now lost), is redescribed. Sixteen forms are illustrated with photographs.

INTRODUCTION

The collections made in Costa Rica after the completion of my work on "The Frogs and Toads of Costa Rica," * include a large number of Amphibia. Certain of these have been studied and the results published in two supplemental works.** Others remain unstudied.

In this, a third supplement, the following species are treated:

Bufo holdridgei Taylor
Bufo leutkenii Boulenger
Bufo melanochloris Cope
Dendrobates auratus Girard
Dendrobates typographus Keferstein
Dendrobates granuliferus sp. nov.
Eleutherodactylus monnichorum Dunn
Eleutherodactylus taurus sp. nov.
Hyla zeteki Gaige
Hyla boulengeri Cope
Hyla microcephala microcephala Cope

* The Frogs and Toads of Costa Rica, Univ. Kansas Sci. Bull., vol. 35, pt. 1, no. 5, July 1, 1952, pp. 577-942, figs. 1-69.

** Additions to the Known Herpetological Fauna of Costa Rica with Comments on Other Species. No. I. Univ. Kansas Sci. Bull., vol. 36, pt. 1, no. 9, June 1, 1954, pp. 597-639, figs. 1-12; and
Additions to the Known Herpetological Fauna of Costa Rica with Comments on Other Species. No. II. *ibid*, vol. 37, pt. 1, no. 13, October 15, 1955, pp. 499-575, figs. 1-18.

Hyla picadoi Dunn
Hyla monticola Cope
Hyla gabbi Cope
Hyla alvaradoi Taylor
Hyla pseudopuma Gunther
Hyla legleri sp. nov.
Hyla dulcensis sp. nov.
Hyla eleachroa Cope

TAXONOMIC TREATMENT

Bufo holdridgei Taylor

(Fig. 1)

Bufo holdridgei Taylor, Univ. Kansas Sci. Bull., vol. 35, pt. 1, no. 5, 1952, pp. 607-609, fig. 3, (type locality, approx. 7500 ft., Volcán Barba Western Slope, Heredia Province, C. R.)

The type locality was revisited in 1952 by John Baker and me, but we encountered, unexpectedly, such very cold and wet weather

FIG. 1. *Bufo holdridgei* Taylor. KUMNH No. 30885. Type. Western Slope Volcán Barba, 7500 ft. elev., Heredia Province, C. R. Actual snout-vent length, 28 mm.

that we were practically incapacitated, and as a result, obtained no adequate collections there. The species was not rediscovered. A photograph of the type is given.

Bufo luetkenii Boulenger

(Fig. 2)

Bufo luetkenii Boulenger, Ann. Mag. Nat. Hist., ser. 6, vol. 8, 1891, pp. 455-456 (type locality, Cartago, Costa Rica).

A specimen, KUMNH No. 32810, taken by me at the Maribella Hotel, at the base of the Puntarenas Peninsula, Puntarenas Province, Costa Rica, is a female and not fully mature, but it seems to agree with the type description of *Bufo leutkenii* in essential points. Al-

FIG. 2. *Bufo leutkenii* Boulenger. KUMNH No. 32810, Maribella Hotel, at base of the Puntarenas Peninsula, Puntarenas Province, C. R. Actual snout-vent length, 51 mm.

though a young specimen, the cranial crests are strongly developed. The supraorbital crests curve strongly, and the supratympanic and postorbital crests are high and sharply defined. The snout is compressed, truncate, with a distinct vertical ridge on tip. The parietal crests, if extended, would form a right angle.

The parotoid gland is slightly oval with a surface area not or slightly exceeding that of the tympanum. The diameter of the tympanum is slightly less than half the length of the eye-opening. The interorbital distance is slightly greater than the width of an eyelid. When the leg is laid forward the tibiotarsal articulation reaches the tympanum. A few scattered, somewhat larger tubercles are mixed with smaller tubercles on dorsum.

The subarticular tubercles on fingers are single, except the distal one on the fourth finger, which is double. The first finger is longer than the second. The palmar tubercle is large, somewhat oval, while the inner metacarpal tubercle is less than half as large in area.

The toes, unlike the type, are distinctly less than half webbed (in adult type half webbed).

When the legs are folded the heels do not touch. Two metatarsal tubercles are present, both relatively small, the inner distinctly the larger. A row of tubercles replaces the tarsal fold.

The figure given here shows the dorsal marking. The median line is only moderately distinct, while the V-shaped mark is strongly defined, the other markings less so. The parotoids are faintly yellowish, as are the tubercles below the tympanum. The cranial crests are brown, the eyelids gray. The venter is cream without any pigmentation.

This species is probably most closely related to *Bufo gemmifer* Taylor of southern Mexico.

Bufo melanochloris Cope

(Figs. 3, 4)

Bufo melanochloris Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, 1875, p. 100 (type locality "Eastern Costa Rica").

The following specimens are in the collection: KUMNH Nos. 28356, 30280-81, 32817-19, Turrialba, Cartago Province; Nos. 30275-79 Pacuare (between Moravia de Chirripó and Turrialba on the Pacuare River, Limón Province.

The largest specimen I have seen is No. 32819 ♂ from Turrialba, measuring 58 millimeters from snout to vent.

The vocal slits are paired. The undersides of the hands, feet, tarsi, chin, throat, and breast are blackish or brownish black with

some dark reticulation on the venter. Much of the underside of thigh is cream. A row of sharp tubercles, along the edges of the tarsus, is cream, in sharp contrast to the blackish color of the underside of the tarsus. The tarsal joint reaches the anterior edge of the eye. The parotoids are double the size of the tympanum.

FIG. 3. *Bufo melanochloris* Cope. KUMNH No. 32819. At bridge across Río Reventazón, Turrialba, Cartago Province, C. R. Actual snout-vent length, 59 mm.

When the legs are folded the heels overlap one millimeter. The toes are approximately one-third webbed.

A specimen of a small toad, No. 32809 (45 millimeters in snout-vent length), taken at the Esquinas Forest Preserve (between Palmar and Golfito) Puntarenas Province, while presenting many characters of *melanochloris*, differs in several significant points. It

is compared with my largest female *melanochloris*, measuring 42 millimeters from snout to vent.

The front part of the snout is rounded, not forming a noselike elevation with slightly depressed areas on each side; the canthi are rather sharp-edged, extending to the anterior level of the nostril, not flattened or thickened and terminating posterior to nostril; the supraocular ridge is continuous with the parietal ridge, not forming an angle where it is joined by the postocular ridge; the ridges are separated a smaller distance, and somewhat less elevated; the

FIG. 4. *Bufo melanochloris* Cope. KUMNH No. 32809, Esquinas Forest Preserve, between Palmar and Golfito on railway. Actual snout-vent length 46 mm.

parotoids are very small, about half the size of those in *melanochloris*. The distance between the parietal and the supratympanic ridges is greater, (5 mm.: 4 mm.) and the area between is less excavated. The choanae when seen from below are nearly two-thirds concealed by the overhanging palatal shelves (not completely visible as in *melanochloris*); the region back of the eye is less elevated (6.5 mm.: 7 mm.) and the tympanum is a half closer to the supratympanic ridge.

The color is brown rather than gray green and black. The narrow interorbital band is present but otherwise the head is uniform light chocolate-brown except for a tiny cream spot below the eye. A discrete median gray-white line is present on the back behind occiput. Underside of limbs dark, the tubercles under hand and foot cream, in strong contrast. The back of the thigh is nearly uniform blackish-brown. The cross-bands on the limbs are smaller.

I suspect that the forms are related. Further material will demonstrate whether or not it represents a western subspecies of *melanochloris*. A figure of the specimen is given.

Dendrobates auratus (Girard)

This species has a relatively wide distribution in Costa Rica, occurring on both coasts. In living specimens there were slight color differences, and some difference in the pattern of the marking between specimens from southwestern Puntarenas Province and those on the east coast. The terminal discs on the digits average a little smaller.

One small population in the region of La Lola, Limón Province has the digital pads larger than those from the eastern coastal areas.

Specimens in the collection are from the following localities: KUMNH, Nos. 36051-57, 36348-54, Suretka; Nos. 33058-72 Mountain Cow Creek, near Banano; Nos. 33090-91, Limón; Nos. 33073-81, 33104, La Lola. All the above are from Limón Province. KUMNH, Nos. 33092-33103, Palmar; Nos. 30382-30389 Esquinas Forest Reserve on railway between Palmar and Golfito; both lots, Puntarenas Province.

Dendrobates typographus Keferstein

(Fig. 5, lower three)

This diminutive species is quite variable in color, especially as regards the extent of the areas occupied by red and blue. In Costa Rica it is presumably confined to the eastern lowlands. The following numbers are in the KUMNH collection: Nos. 24884-901, 30451-58, 33048-56, Los Diamantes, near Gúapiles; Nos. 33036-47,

La Lola; 33057 Mountain Cow Creek; Nos. 35935-89, 36051-103, 36355-60, 36544-50, Suretka, all from Limón Province. KUMNH Nos. 36523-43, Puerto Viejo, Heredia Province.

In the Suretka area, the outer sheath, that is shed from the leaves of a small palm, is curved so that it may accumulate rain water. This is used as a place for the deposition of eggs of this small species. More than 25 such "breeding ponds" were counted in a small area. The eggs were for the most part recently laid, although a few "ponds" had recently hatched larvae. The date was July 3, 1954.

Dendrobates granuliferus sp. nov.

(Fig. 5, upper three)

Type: KUMNH No. 43874; obtained on low mountains north of the Río Diquis, about 3 miles north of Palmar, Puntarenas Province Costa Rica, Sept. 3, 1952, by Edward H. Taylor.

Paratypes: KUMNH Nos. 43875-43880 topotypes, collected by John Baker, Paul Allen, and Edward H. Taylor.

Diagnosis: A diminutive toothless toadlike species characterized by having the entire dorsal and lateral surface of body and upper surface of femur covered with relatively large pustular granules, those in the dorsolateral regions largest; venter and greater part of undersurface of thigh with similar but somewhat flattened granules; discs on digits widened, their dorsal surface divided by an indefinite groove; hands and feet lacking trace of web. Body orange, sometimes shading to brick-red; the hind limbs usually greenish blue.

Description of type: Head a little narrower than body, its greatest width (7.5 mm.) almost equal to its length (7.7 mm.); canthus rostralis absent or very broadly rounded; snout short, the tip broadly rounded; nostrils lateral, not visible, seen from above; loreal region nearly vertical, slightly excavated; distance of nostril from eye (2 mm.) less than distance from midpoint of upper lip; distance between nostrils (3.1 mm.) greater than interorbital distance (2.5 mm.); width of eyelid (2.2 mm.) less than interorbital distance; length of eye-opening (2.7 mm.) greater than length of snout but shorter than its distance from tip (3 mm.); lower part of tympanum visible (when exposed by removal of skin and muscle, it measures 1.6 mm. high, 1.25 mm. wide on paratype).

Palate excavated, the small choanae completely concealed by overhanging palatal shelves when seen directly from below; no vomerine or maxillary teeth; tongue elongate, free on sides, posteriorly widened and free for two thirds of its length; vocal sac

FIG. 5. Upper series of three, *Dendrobates granuliferus*. Left to right, KUMNH No. 43876, actual snout-vent length 22 mm., No. 43877, 22 mm., 43874, Type, 23 mm. All from 3 mi. N. Palmar, Puntarenas Province.

Lower series of three, *Dendrobates typographus* Keferstein. Left to right, KUMNH No. 33040, La Lola, Limón Province; 23 mm., No. 24893 Los Diamantes, 21 mm., No. 33038, La Lola, Limón Province, 24 mm.

indicated externally by slight folds, the vocal slits large, their edges somewhat thickened.

Arm with wrist reaching end of snout; fingers completely free, with widened terminal discs, that of the third finger more than twice width of first, a fourth wider than second and fourth; first finger distinctly shorter than second; inner metacarpal tubercle small, smaller than the flattened subarticular tubercles but only about one fifth of the area of the large single palmar tubercle; a small distinct tubercle somewhat behind wrist on under surface of arm; discs normally without a terminal groove (if somewhat dehydrated a groove appears); upper surface of discs (except first) with two rounded elevations separated by a groove or depression.

Leg short, the tibiotarsal articulation reaching to latter fourth of eye; when legs are folded at right angles to body, the heels touch; toes completely without webs; toes with discs, that of fourth toe equally as large as discs on second and fourth fingers; the third extends two thirds of its length beyond fifth; first toe very short, inner metatarsal tubercle large, somewhat elongate; outer larger, rounded; an indistinct tubercle on distal part of tarsus and a slight short inner tarsal ridge ending abruptly in a rounded tubercle; upper surface of discs on third and fourth toes divided by a depression, absent in other toes;

Head with flattened tubercles on occiput and interorbital region remainder glassy smooth; body and sides with irregular-sized pustular granules; arm entirely smooth; thigh with granules on upper surface; inner part of posterior surface of thigh and most of the posterior half of the ventral surface, the upper side of tibia and tarsus, with slight suggestion of granules; remainder of limb glassy smooth; venter strongly granular; breast minutely roughened; the throat and chin with indistinct longitudinal folds, slightly roughened and pitted; no supratympanic fold; upper part of eyelids smooth.

Color in life: Above generally orange, the limbs bluish to greenish blue, the color fading completely in a few days, and in preservative the specimens are nearly black, the arms and legs brownish to brownish black; under side of digital discs grayish.

Measurements in mm.: (Nos. 43874 ♂, 43876 ♀, 43880 ♂ respectively.) Snout to vent, 23, 22, 22; width of head (at tympanum) 7.5, 7, 7; length of head (to back of jaw angle); 7.7, 7.6, 7.6; arm, 16.2, 15.2, 15.2; leg, 29, 27.1, 29; tibia, 9.5, 9.2, 9; foot and tarsus, 13.5, 13, 13.5.

Variation: Females have grooves with thickened edges where the vocal slits are present in the male. The dorsal color varies between brick-red and orange, and often the limbs are nearly blue.

Remarks: The specimens were taken from the side of a low mountain north of the Río Diquis about 3 miles north of Palmar, Puntarenas Province. They were moving about on the forest floor in the afternoon.

Aside from the granulation on dorsum and venter, the species differs from *Dendrobates typographus* in having usually larger metatarsal and metacarpal tubercles, the heels not overlapping (overlap at least 2 mm. in *typographus*) and the terminal pads on hands are usually larger. A few specimens of *typographus* may show a few tubercles on the extreme posterior part of venter. The tarsal tubercle is smaller and less conspicuous and the dorsum is usually glassy smooth. The dorsal groove is present on all digital discs except those of inner finger and toe.

The species name is derived from the Latin *granulum*, little grain, and *ferre* to carry.

Eleutherodactylus monnichorum Dunn

(Fig. 6)

Eleutherodactylus monnichorum Dunn, Proc. Acad. Nat. Sci. Philadelphia, vol. 92, Nov. 18, 1940, pp. 105-122, pl. 2 (type locality, Valley of the Velo, Finca Lérida on the slope of Volcán Chiriquí above Boquete).

A series of specimens taken by me at Água Buena, near Cañas Gordas, Puntarenas Province, Costa Rica, July 22, 1954, are referred to this species. They are KUMNH Nos. 37480-37486, taken in forest at an elevation of perhaps less than 2000 ft.

They differ in certain characters from typical *E. monnichorum* and may represent a lowland subspecies. I give herewith a detailed description of one of the specimens, KUMNH No. 37483.

Diagnosis: A medium-sized species of the genus with narrow (often broken) dorsolateral folds or ridges running from near eye to groin; hand without web, the digits without lateral ridges or fringes; fingers with terminal pads, those of the two outer, double the width of pads on two inner digits; two subequal palmar tubercles; inner toes one-third to one-half webbed, the digits usually with a slight lateral fringe; sole without supernumerary tubercles; tibiotarsal articulation reaches several millimeters beyond snout; chin and venter smooth; a broad, nearly uniform light-brown stripe covers head and body between the black dorsolateral folds; canthus rostralis marked, slightly rounded; greatest diameter of tympanum

(♀) about two thirds of the length of eye-opening; tympanum of male about three fourths of eye length; vomerine teeth in two groups, not reaching level of choanae; two vocal slits, the vocal sac not or scarcely indicated externally.

Description of KUMNH No. 37483: Head distinctly wider than the body, the outline forming an oval; canthus rostralis distinct, the edge slightly rounding; snout slightly rounding in lateral profile,

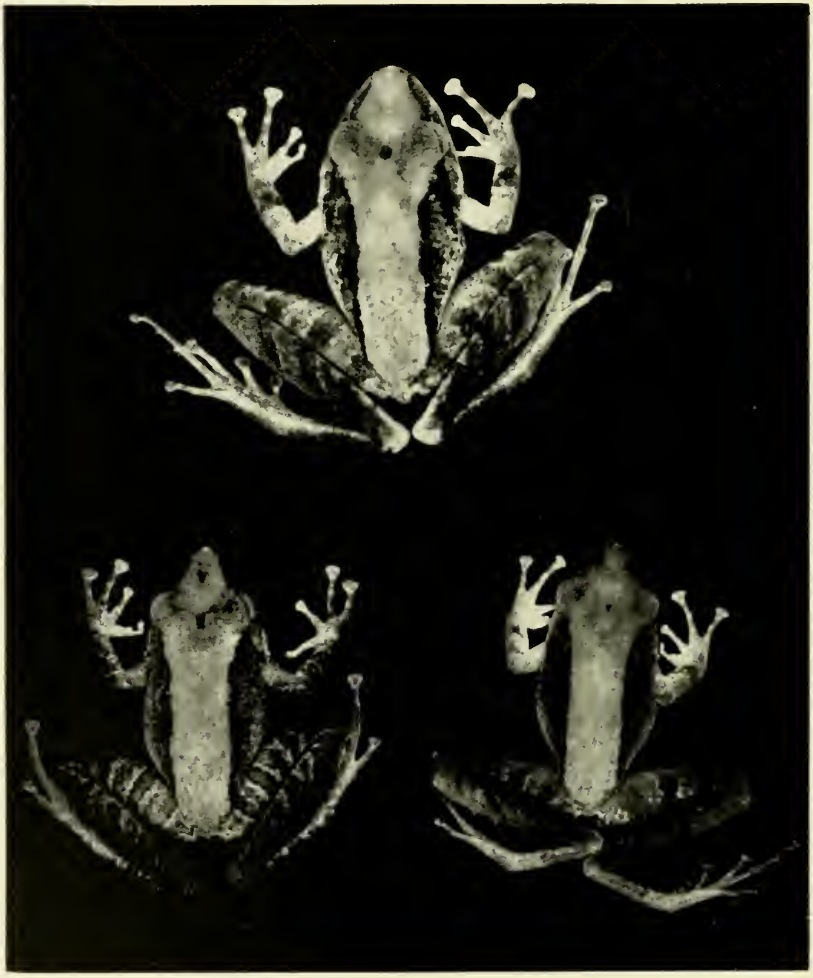

FIG. 6. *Eleutherodactylus monnichorum* Dunn. Upper figure, KUMNH No. 37483, snout-vent length 31 mm.; lower left, No. 37481, 27 mm., lower right, No. 37486, 26 mm. All from Agua Buena, near Cañas Gordas, Puntarenas Province (near Panamanian border).

the nostril distinctly closer to the median point on upper lip than to eye; loreal region shallowly concave, then sloping broadly to the lip; a slightly flattened area between nostrils. Head rather flattened but slightly deeper than snout; interorbital distance very slightly less than the greatest width of an eyelid; a pustule between orbits (usually black in color). Length of eye-opening distinctly less than distance between eye and nostril; tympanum vertically oval, its greatest diameter about two thirds of the length of the eye; a tiny lobule indicated on posterior edge of lower eyelid; a slightly curving, distinct supratympanic fold covers the upper edge of the tympanum and terminates above arm; a small glandular tubercle behind tympanum.

Tongue as broad as long, somewhat notched posteriorly, free behind for nearly one third of its length, and likewise free on the sides. (Vocal slits in males do not reach forward to the middle level of tongue.) Vomerine teeth on two somewhat triangular elevations beginning behind posterior level of the small choanae, and extending back as far as the level of the transverse palatal ridge.

Arm rather short, laid forward, the wrist reaches the tip of snout; first finger slightly shorter than second with a somewhat smaller terminal pad; the terminal pads of two outer fingers more than double the width of the pad on second; subarticular tubercles prominent; inner metacarpal tubercle larger than palmar tubercles; outer palmar tubercle divided into two subequal parts; four supernumerary tubercles on palm; a row of indistinct tubercles under forearm.

Legs long, the tibiotarsal joint reaching beyond the tip of the snout about half the length of the tibia, when limb is laid forward; when legs are folded, the heels overlap about five millimeters; inner metatarsal tubercle flat, about three times the area of outer tubercle, toes with terminal pads, intermediate in size between those of second and third fingers, those of the three middle toes larger than those of the outer finger; three inner metatarsals largely separated by a web, the two outer metatarsals not so separated, resulting in a very short web between two outer toes; inner toes webbed for nearly half their length, the digits for the most part with narrow lateral fringes; subarticular tubercles equal to or a little smaller than those on fingers; no tubercles on sole.

Above, skin appearing smooth generally save that under a lens a fine granulation is observable; the dorsolateral folds partly broken

into elongate warts of variable width; sides finely granular with some pustular tubercles, two of those above arm largest and black in color; chin and venter smooth; ventral part of thigh, and area about vent, granular; a slight abdominal fold outlines the "ventral disc."

Color: Above, the top of snout, interorbital region, occiput, and dorsum nearly uniform light brown to yellowish brown (approaching fawn in some specimens); a black dot between orbits; eyelids darker brown; dorsolateral fold and area just below, black; a black spot behind eye covering the supratympanic fold, and a few small black spots on upper surface of arm; fingers with dark and light bands; forearm with a single dark band; thigh and tibia with three or four dark brown or blackish bands; toes not banded; blackish on underside of foot and tarsus; venter dull flesh-white with scattered pigment on chin and breast; loreal region blackish, with some cream spots; one or two black spots on outer part of front face of thigh; back of thigh brownish with lighter flecks; a black area surrounding vent with some light flecks evident.

Measurements in mm. of *Eleutherodactylus monnichorum* Dunn

Number	37483	37481	37486	37482	37484	37480	37485
Sex or age	♀	♀	♂	♂	♂	♂	yg
Snout to vent	31	27	26	26	25	25	17.5
Head width	13.6	12	10.2	11	10.2	10	7
Head length	14	13	12	12.2	12	12	8.7
Axilla to groin	13	12	11	11	11	11.2	8.2
Snout to arm	11.2	10.8	10	10	10.4	10	8
Arm	21	17.5	16	15	17	16	11
Leg	67	55	49.3	48.2	48	48	32
Tibia	21.5	19	17	17	17	16	11
Foot and tarsus	29.2	25	21	21	21	21	14.2

Variation: The dorsal coloration is similar in all. Two males have the sides almost uniformly dark while in another the color is rather light. The black interorbital spot is absent in one younger specimen.

The males have the first finger strongly swollen at the base and vocal slits are evident in the floor of the mouth. They would appear to be adult or nearly so.

Remarks: My specimens differ from the description of the type of *E. monnichorum* as follows: distance of nostril to tip of snout one third of the distance from the eye (not one half); there is no ridge present across the interorbital region, a single elongate wart on the scapular region (not "two parallel elongate warts on each scapular region running in and back from corner of head the outer sometimes in contact with, or a part of the dorsolateral fold"); the terminal pads on outer fingers are distinctly smaller than the tympanum in either males or females (not "as large as the tympanum in adult females"); eye length distinctly less than its distance from nostril (not "eye equals its distance from nostril").

Perhaps the most significant differences are the absence of the interorbital ridge, the eyelid wider than interorbital distance, and smaller digital pads. It is, of course, possible that my series does not represent fully grown specimens and the differences are those of age. Until this is determined the status of these specimens cannot be determined beyond question.

The type locality is no considerable distance south of Agua Buena, probably not more than 25 miles in a straight line.

Eleutherodactylus taurus sp. nov.

(Fig. 7)

Type: KUMNH No. 43866, taken at Golfito, Puntarenas Province, Sept. 6, 1953 by Edward H. Taylor.

Paratypes: KUMNH Nos. 43868, 43872, collected Palmar, Puntarenas Province, Sept. 2, 1952, by Edward H. Taylor; Nos. 43867, 43869-43870, 43871, 43873, Golfito, Sept. 2-6, 1953, collected by Edward H. Taylor and John Baker.

Diagnosis: A large somewhat toadlike form of the *rugulosa* group, characterized by a diminutive tympanum, its greatest diameter two-and-a-half times in length of eye; fingers free; toes with lateral fringes and webs extending between separated metatarsals, the depth of the web equaling half of the length of the toes; slightly widened finger discs, those on toes larger, but still smaller than tympanum; tympanum separated from eye by a distance equal to its vertical diameter; a strong tarsal fold; inner and outer metatarsal tubercles present; vomerine teeth on two elevated bony ridges behind posterior level of choanae, the teeth on the posterior borders; tongue free behind for one fourth of its length and free on sides;

choanae about as large as openings to Eustachian tubes. Skin finely granular, rough; eyelids wider than the interorbital distance. Males with elongate vocal slits and vocal sac.

Description of type: Head oval in outline, the width (29.5 mm.) greater than the length (26 mm.); canthi rostrales distinct, if projected would form an angle much in advance of nostril; loreal region slightly excavated, the upper part nearly vertical, then sloping broadly to lip; distance between eye and nostril (8 mm.) a little greater than distance of nostril to median point on upper lip (7

FIG. 7. *Eleutherodactylus taurus* sp. nov. KUMNH No. 43867 ♀, Golfito, Puntarenas Province. Actual snout-vent length, 76 mm. The curious mark on the back is seemingly caused by a scar.

mm.); tip of snout rounding, extending two millimeters beyond mouth; interorbital distance (5.5 mm.) less than width of an eyelid (7.5 mm.). A strong thick supratympanic fold overhangs tympanum; running nearly straight back from eye, then forming an angle, turns downward to above arm; rim of tympanum incomplete above; tympanum small (4 mm. x 3 mm.); length of eye-opening (9.1 mm.) a little greater than its distance from nostril; tympanum separated from eye by a distance of four millimeters.

Vomerine teeth along back edge of two closely approximated, elevated triangular ridges, which reach forward nearly to posterior level of choanae; palatal glands open in middle of palate about midway between anterior level of choanae and anterior end of palate; tongue about as long as wide, free on sides, free posteriorly for about one fourth of its length. (Male with vocal sacs, the slits reaching forward to near back level of tongue.)

Fingers lacking trace of web but with distinct lateral ridges, the terminal pads of fingers a little wider than the digits, those of two outer fingers larger than the two inner; a strongly elevated inner metacarpal tubercle; palmar tubercle much larger, somewhat bifid; subarticular tubercles moderately large, and four small supernumerary tubercles on palm (metacarpals); tibiotarsal articulation reaching nostril.

Leg moderate, the metatarsals, except outer, partly separated by a web, the web nearly half as long as digits measured to pads; terminal discs on three middle toes larger than any finger discs; an elongate elevated inner metatarsal tubercle about one half of length of first toe; a small outer tubercle; fringes on toes reaching from web to disc, those of third and fourth toes folded down; no supernumerary tubercles on sole; a sharply defined tarsal fold extends three fourths of the length of tarsus; heels touch when limbs are folded at right angles.

Skin above with rather fine granular pustules, and a few somewhat larger pustules growing more numerous and prominent laterally; eyelid strongly pustular, as are dorsal parts of arms and legs; chin slightly wrinkled longitudinally; breast smooth; venter transversely wrinkled with some indistinct granulation; ventral disc scarcely defined; much of area under thighs completely smooth save in region below and near vent, which is finely granular.

Color: Above, dark lavender-brown with a darker interorbital mark and some dim traces of other darker marks; lip with four in-

distinct cream blotches and one or two cream flecks below eye; indistinct spots or bands on thigh, tibia, and tarsus; upper parts of hand and foot with some darker marking; chin, breast, venter, lower part of sides, underarm, ventral part of thighs, and concealed part of tibia, cream-white. Undersurface of foot dark purplish-lavender; tubercles light lead color; most of underpart of hand similar; posterior part of thigh dark lavender-brown with whitish flecking or reticulation.

Measurements in mm. of *Eleutherodactylus taurus* sp. nov.

Number	43867	43866	43868	43869	43870	43872	43871	43873
Sex	♀	♀	♀	♀	♀	♀	♂	♀
Snout to vent	76	72	65	62	53	43	42	41
Width of head	31	29.5	28	27	24	19	18	17.5
Length of head	29	26	26	25	21	18	18	17
Snout to arm	28	28	22.5	23	22	18	16	15
Axilla to groin	30	26	27	23	22	16	14.8	15
Arm	43	43	40	36	34.5	27	27	24
Leg, from vent	115	116	105	98	92	69	70	62
Tibia	36	35	34	32.5	29	22	21.5	21
Foot and tarsus	49	49	46	45	40	29	31	28.5

Variation: No. 43867 has the dorsal spots a little more distinct, and the banding on arms and legs is quite distinct. Some dark flecks appear on the edge of the lower jaw. Certain of the other paratypes have the limbs paler and the posterior part of the tibia and tarsus show whitish areas between the bands. To some extent this is true in the male specimen but in the smallest female the light areas are scarcely discernible.

The tympanum of the male is larger proportionally. It is subcircular and the greatest diameter is a little more than half the length of the eye-opening; the outer metatarsal tubercle is proportionally more elevated.

The presence of the vocal sac separates this form from other large species of the same group except *Eleutherodactylus fleischmanni.*

The tympanum is larger in that species (in male nearly as large as eye). The venter is smooth and there is less webbing between the toes; the dorsum is less rugose. There is considerable difference in the vertical range. *E. fleischmanni* is known from 4000 to 6500 ft. elevation; *E. taurus* is from sea level.

The name is derived from the Latin *taurus* = *bull.*

Hyla zeteki Gaige

Hyla zeteki Gaige, Occ. Papers Mus. Zool. Univ. Michigan, no. 207, 1929, pp. 4-6 (type locality, Caldera Valley above Bouquete, Chiriquí Department, Panamá).

Three more specimens of the diminutive *Hyla zeteki* were taken, as follows: KUMNH Nos. 36480-81, La Palma, San José Province; No. 36942, Vara Blanca, Heredia Province. The latter specimen is a female containing numerous, much-pigmented eggs. The two former are males. The base of the first finger is swollen nearly three times the width of the antepenultimate phalanx, but there are no spinous areas indicated. Both males are infected with the larvae of a dipterous insect, No. 36481 having three. They lie under the skin along the sides of the abdomen, and one under the thigh skin. The other male has two larvae. The largest larvae are two millimeters in length.

Hyla boulengeri (Cope)

(Fig. 8)

Scytopsis boulengeri Cope, U. S. Nat. Mus. Bull. No. 32, 1887, pp. 12-13 (type locality, Nicaragua).

A series of male specimens of *Hyla boulengeri* from Suretka, Limón Province, differs from a specimen from Turrialba (1900 ft.) in having more pigment on the chin and throat and on the underside of thighs, tibia, and feet. There are two prominent pointed tubercles on the area immediately above the vent. The interorbital tubercles are distinct; a row of small tubercles curving across the occiput and reaching eyelids are usually blackish, outlining a somewhat darker area. There is a row of tubercles (often broken) under the forearm. A pair of somewhat larger tubercles are present on the canthi. The nostrils are somewhat more elevated.

Specimens in the collection are as follows: KUMNH No. 24741 Turrialba, Cartago Province; Nos. 36482-88, 36699 Suretka, Limón Province; No. 37031 Banano, Limón Province; Nos. 34104-34106 from 15 km. WSW San Isidro del General, San José Province.

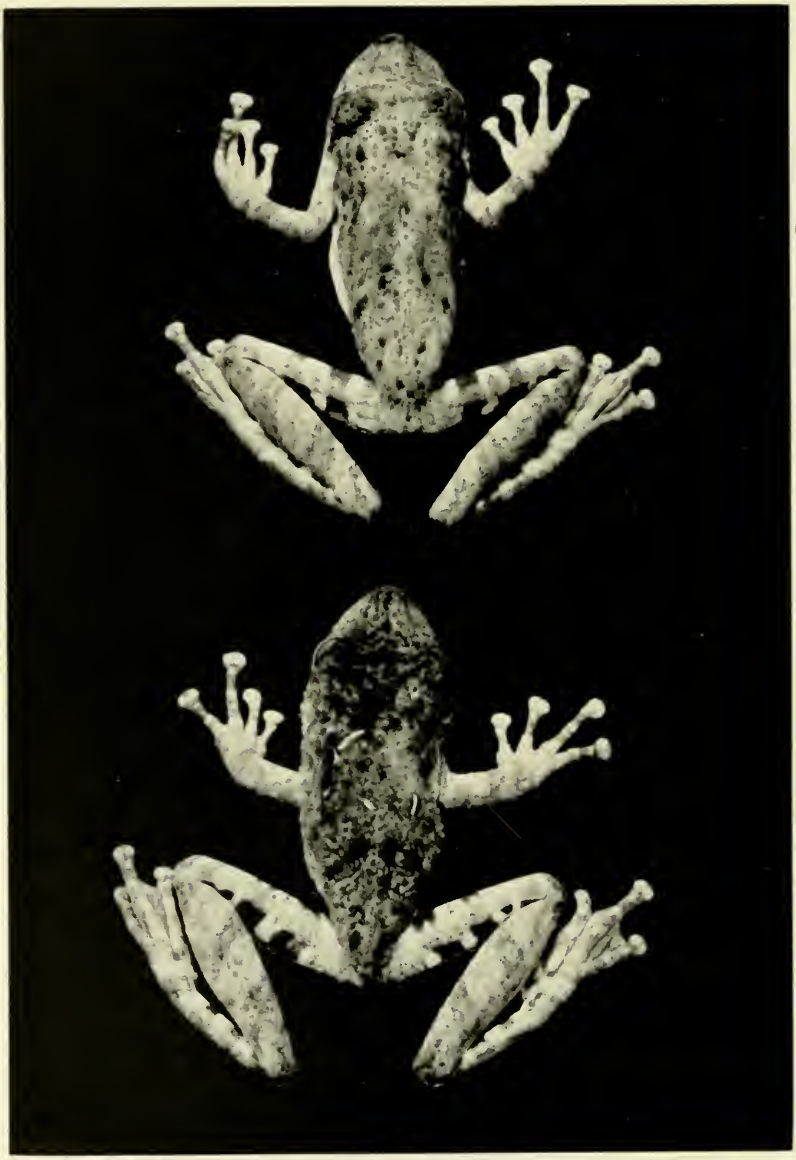

FIG. 8. *Hyla boulengeri* (Cope). Upper figure, KUMNH No. 34106, snout-vent length, 45.4; lower figure, No. 34105, snout-vent length, 45. Both from 15 km. WSW San Isidro del General, San José Province, C. R.

Hyla microcephala microcephala Cope

(Fig. 9)

Hyla microcephala Cope, Proc. Amer. Phil. Soc., Apr. 1886, vol. 23, no. 122,, pp. 281-282 (type locality, Department of Chiriquí, Panamá, "along a mountain stream").

A large series of specimens of *Hyla m. microcephala* KUMNH Nos. 32172-32206 was taken at Golfito, Puntarenas Province, and represent, I believe, the first record of the species for Costa

FIG. 9. *Hyla microcephala microcephala* Cope. Upper figure, KUMNH No. 32184 ♂; actual snout-vent length, 22.2 mm; lower figure, No. 32172 ♀, length, 28.6. Both from Golfito, Puntarenas Province, C. R.

Rica. Specimens were breeding in small temporary pools one to five inches deep, September 6-9, 1952.

Diagnosis: A diminutive species characterized by a very much widened third finger; a pair of brown lines from anterior part of eye running down middle of back; a narrow dorsolateral brown line; toes four-fifths webbed; outer fingers one-third to two-fifths webbed; head small; vomerine teeth between choanae not or scarcely extending behind their posterior level.

Description of KUMNH No. 32172: Head width (8.5 mm.) slightly greater than length (8.2 mm.), not or scarcely greater than body width; width of eyelid (1.9 mm.) smaller than interorbital width (2.6 mm.); canthus rostralis rounded, curving; loreal region slightly concave; distance between eye and nostril (2.2 mm.) equal to distance from nostril to median notch in upper lip, much less than length of eye (3.1 mm.); tympanum distinct its diameter (1.5 mm.) twice in length of eye-opening; separated from eye by a distance less than its diameter; its upper part concealed by the distinct supratympanic fold.

Vomerine teeth abnormal (normally vomerine teeth on two low moundlike swellings between choanae, closer to each other than to choanae; usually smaller than choanae and scarcely reaching their back level); tongue longer than wide, large, flat, narrowly free behind and along sides, with a slight median notch behind; palatal groove distinct, a little closer to anterior level of choanae than to front of palate; (male with a large external vocal sac; vocal slits large).

Arm brought forward, the wrist reaches end of snout. A web remnant between two inner fingers; between second and third, two-fifths webbed, to pad of second; between outer fingers about one-third webbed to pad of outer finger. Digital pads of three outer fingers large, subequal, of inner finger smaller; distal subarticular tubercles single on first and second fingers; lateral folds on digits somewhat thickened; a large flat inner metacarpal tubercle; palmar tubercle smaller, double or bifid; no distinct skin-fold under forearm; seen from above, fourth finger widened.

Leg brought forward the tibiotarsal joint reaches the anterior level of eye. Toes almost entirely webbed to digital pads, which are smaller than those on fingers, except pad on inner; inner metatarsal tubercle elongate, oval, flattened; outer tubercle if present, indistinct. When legs are folded at right angles the heels overlap three millimeters.

Skin on head, sides, and upper part of limbs smooth; a somewhat thickened, nearly straight supratympanic fold, continuing straight back from eye, can be traced to above arm onto side (usually cream colored); chin smooth (in males a very ample vocal sac); venter with distinct granules; much of undersurface of thighs granular; a slight fold across breast interrupted mesially; small axillary web present; area about vent smooth; the muscles surrounding vent give the area an inflated appearance.

Color in life: On exposed surfaces, cream with scattered brownish pigment but forming two moderately distinct lines on body from eye to end of rump; a more or less distinct cream line from tip of snout along canthus rostralis, continuing behind eye to near groin; upper part of tympanum pigmented; lip cream, the loreal region brownish; a brown line present below the cream dorsolateral line, becoming obsolete posteriorly; venter and concealed surfaces cream or creamy flesh.

Measurements in mm: (KUMNH Nos. 32172 ♀, 32173 ♀, 32176 ♂, 32180 ♂, respectively): Snout to vent, 28, 28.7, 24.8, 25; width of head 8.5, 8.7, 8, 8.1; length of head, 8.2, 8.2, 7.7, 8; arm, 17.2, 18, 14, 13.5; leg, 43, 46, 37.5, 39; tibia, 14.8, 15.3, 12.8, 13; foot and tarsus, 20, 21.5, 17.6, 17.2.

Remarks: This species appears to replace *Hyla underwoodi* in southwestern Costa Rica. The latter species is common farther north in the northern part of Puntarenas and Guanacaste Province, where I obtained large series in 1953 and 1954.

It differs from *H. underwoodi* in having a different color pattern, with hand, foot, and digits more slender. *Hyla phlebodes*, a member of the same group, known from the eastern Meseta Central drainage areas, is not uncommon at Turrialba, Cartago Province. It is a smaller species with a distinctly broader head and proportionally larger eyes. A brown interorbital line is present.

The widened fourth finger is a characteristic of this group of *Hyla*.

Hyla picadoi Dunn

Hyla picadoi Dunn, Copeia 1937, no. 3, p. 164 (type locality, a little above farm of Manuel Acosta 2140 m., Volcán Barba, Heredia Province).

A specimen of this species, KUMNH No. 36127, has been found in the Talamanca range at the Bosque Nacional (Pan American Highway), elevation about 8000 feet. The paired denticulations in the front of the lower jaws, while evident are low.

Hyla monticola Cope

(Fig. 10)

Hyla punctariola monticola Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, 1875, p. 106 (type locality "Cordilleras at from 5000-7000 feet" elevation, slopes of Pico Blanco, Costa Rica).

The type of this species is presumably lost. The original specimen was probably in bad condition, since it was not figured and the type description is very brief and inadequate.

FIG. 10. *Hyla monticola* Cope. KUMNH No. 36764 ♀, Cocales Creek, Suretka, Limón Province, C. R. Actual snout-vent length, 43 mm.

A species of *Hyla* which I took at Suretka in southeastern Costa Rica, at an elevation of perhaps 300 feet, agrees with the color description of *H. monticola* in being transversely banded on dorsum, a condition not normally found in other Costa Rican frogs. Other similarities and differences are discussed following the description of this specimen, No. KUMNH No. 36764 ♀, collected June 26,

1954, along Cocales Creek, Suretka, Limón Province, Costa Rica, by Edward H. Taylor.

Diagnosis: Related to *Hyla gabbi.* Eye longer than the distance between eye and nostril; width of eyelid less than the interorbital distance; canthus rostralis, distinct, rounded; greatest diameter of tympanum about one half of the length of eye; skin glassy smooth; tympanum smooth; a supratympanic fold; area about vent smooth; chin indistinctly granular, breast venter and under thighs with strong granules; outer fingers two-thirds webbed; two inner fingers webbed only at base; tibiotarsal articulation reaches one millimeter beyond snout; snout-to-vent length, 43 mm. Whitish on chin; venter, and under thigh, without pigment; under part of foot darkly pigmented; hands below dirty white; brownish gray above, the back with four black bars; the tibia strongly banded, the thighs less distinctly so.

Description: Female. The width of head (17 mm.) is greater than length (14.1 mm.); canthus rostralis distinct, rounded, if projected would form an angle with its fellow between nostrils; loreal region slightly concave, sloping rather sharply to lip; snout rounded at tip, scarcely extending beyond the edge of lip; nostril a fourth nearer to the median point on upper lip than to eye; length of eye-opening (4.8 mm.) greater than distance from eye to nostril, (4.15 mm.), shorter than snout length (6 mm.); tympanum, 2.1 mm. in vertical diameter, 1.9 mm. longitudinal diameter; supratympanic fold curving up slightly, runs from eye, back to above arm, separated from tympanum posteriorly; tongue about as long as wide, not or scarcely notched behind, without a free posterior or lateral part; choanae large (1.3 mm.); a pair of strongly elevated ridges directed backward, arise from anterior inner edge of choanae extending back beyond the level of the middle choanae, touching mesially, and each bearing at least six teeth posteriorly; palatal glands open separately much anterior to level of choanae, near midline of the palate without forming a transverse groove; openings of Eustachian tubes smaller than choanae.

Arms with a small axillary web; upper arm slender, the forearm much heavier, three outer fingers two-thirds webbed; two inner fingers with a small basal web, the digits with slight lateral ridges or fringes to tip; inner metacarpal tubercle elongate, narrow, compressed; two small subequal palmar tubercles; subarticular tubercles small, that on outer distal joint of fourth finger double; palm with numerous tubercles; leg long, the tarsal joint extending about a millimeter beyond tip of snout when leg is brought forward; toes fully

webbed, the web reaching bases of terminal discs, that on fourth toe somewhat narrowed toward the disc; discs on three outer fingers larger than those on toes, that on inner finger smaller than those on toes; metatarsal tubercle elongate, compressed, extending out from edge of foot; no outer tubercle; a slight lateral fringe on outer edge of outer toes; a distinct tarsal fold. Skin above shiny smooth; sides somewhat wrinkled, with granules on lower part; chin nearly smooth; breast indistinctly granular; belly with strong granules; under thigh granules larger, a few with small median dark dots; an area about vent smooth; an indistinct groove from behind vent passing down under thigh; tympanum smooth without granules.

Color: Above rather brownish to lead-gray with frontal region somewhat more brownish; a dark band between eyes, one across scapular region, one across the middle of back and one across the sacrum; tympanum brownish; an area below eye with less pigment; sides lighter with indication of some lighter spots in the groin; front of thigh nearly uniform light gray; back of thigh similar; top of thigh with some darker markings; tibiae with five blackish bars; foot dark gray above; foot dark below with considerable pigment; hand whitish below. The upper arm is white save for a dim line of grayish pigment on its outer surface.

Measurements in mm.: Snout to vent, 43; width of head, 17; length of head, 14.1; arm, 26; leg, 74; tibia, 26; foot, 31.2.

Variation: The color as given in the type description follows: "Color light grayish brown with large dark spots forming transverse bars, one between the eyes, one in front of the scapulae, one behind the scapulae, and one at sacrum. Below unspotted white. Limbs with light brown surfaces above; concealed surfaces, pale, unspotted. No inguinal spots; a few specks of brown on the sides."

Other data given on the type are: "Length of head and body .037 m. fingers not entirely free but a web extends between the outer two to the middle of the phalange. The area of the tympanum in the same, is one-fourth that of the orbit. The head is short and wide and the heel extends nearly or quite to the end of the muzzle."

It will be seen that the two specimens disagree in the degree of development of the web on hand, and the absence of the markings on the limbs. One supposes that the specimen was in bad condition perhaps dried or hardened by preservatives so the webbing may have appeared to be absent between some of the fingers.

Until specimens of *H. monticola* are obtained from the type lo-

cality the identity of this specimen may remain somewhat in doubt. The specimen described was obtained from a shrub in the shallow, fast-flowing Cocales Creek at Suretka. *Hyla gabbi* was breeding in the stream as were certain other species of amphibians.

Hyla gabbi Cope
(Fig. 11)

Hyla gabbi Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, 1875, p. 103 (type locality, near Sipurio, Limón Province, SE Costa Rica).

Specimens of this large *Hyla* are in the collection from the following localities: KUMNH Nos. 28200-201 San Isidro del General and

FIG. 11. *Hyla gabbi* Cope. KUMNH No. 28201, San Isidro del General, San José Province, C. R. Actual snout-vent length, 49.5 mm.

34869-75 Escazú, both, San José Province; No. 37012, IAIA, Turrialba, Cartago Province; Nos. 36764-78, 36791-93 Cocales Creek, Suretka, Limón Province; Nos. 32994-32999, 34863, 34869-75, 36791-93 near Sarchi, Alajuela Province.

Hyla alvaradoi Taylor

(Fig. 12)

Hyla alvaradoi Taylor, Univ. Kansas Sci. Bull., vol. 35, pt. 1, no. 5, July 1, 1952, pp. 882-885, fig. 63 (type locality KUMNH Nos. 31864-65 Moravia de Chirripó, Limón Province, C. R.).

Two specimens, KUMNH Nos. 31864-65, were taken very close to the exact type locality. One, a gravid female, was ready to lay eggs, since some eggs were extruded after capture in the collecting

FIG. 12. *Hyla alvaradoi* Taylor. KUMNH No. 31865, topotype. Moravia de Chirripó, Limón Province, C. R. Actual snout-vent length, 42.3 mm.

bag. The preserved eggs measure from two and one-half to three millimeters in diameter and are without pigment.

Under a lens the dorsum shows a peppering of minute black specks with a few scattered ones on arm and leg. The venter is only faintly granular. The male has a pair of long vocal slits, the

edges of which are whitish. The pigment is slightly more evident on the back, definitely so on the limbs. The white line behind the eye is somewhat less distinct. The curious fold, arching above the vent is present in both of the topotypes.

Coloration in life of No. 31865: "Bright yellow-green above, light lines yellow becoming cream over eyes; eyes bronze-brown; throat and concealed parts of limbs, bluish-flesh; dorsal part of limbs nearly flesh-color, slightly tinted lemon-yellow; under surfaces of hands and feet canary to lemon-yellow; anal fold cream."

The color faded within a few days in preservative, leaving the specimens nearly cream-white.

The life colors of No. 31864 varied somewhat from the preceding as follows: "The dorsum is yellowish with a faint wash of green. The head is bluish green to greenish, generally a little darker on the middle and sides; venter with a whitish or yellowish white area; mental gland yellowish; concealed parts of limbs indefinite flesh; knees bluish; under surface of fingers yellowish, of toes whitish flesh without yellow." Taken June 20, 1952.

The specimens were taken from shrubs at the edge of a small stream only a few meters from where the type was taken.

Hyla pseudopuma Günther

(Figs. 13, 14)

Hyla pseudopuma Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Sept. 1906, pp. 274-275, pt. 72, figs A. and B. (type locality, La Palma, San José Province [1600 m. elev.]).

This species presents problems in identification since the color and pattern is extremely variable, the color changing from nearly blackish to a light olive in a few hours. An hourglass-shaped pattern on the back, considerably darker than the adjoining background, may be present, only to disappear somewhat later. Specimens from near the type locality usually have a dark lateral stripe even when the dorsum is a light olive.

The females are often considerably larger than the males and the "hourglass" pattern may appear as two separate darker-edged marks on a light, often fawn, ground-color.

I am presenting figures of two of these variations.

Specimens have been taken from the following localities: KUMNH Nos. 34973-80 southern slopes of Volcán Poás, elevation *circa* 6800 ft., Alajuela Province; Nos. 36583-96 "in bromelias," Vara

Blanca, southeastern slopes, Volcán Poás, Heredia Province; Nos. 36597-600, La Palma between Volcán Barba and Volcán Irazú 4800 ft. (in bromelias), San José Province; Nos. 34981-84 Finca Montechristo, Volcán Barba, (south slope), Heredia Province; Nos. 28192, 32276-32279, Cinchona (Isla Bonita), 4000-5500 ft. elev., Heredia Province; Nos. 32280-81 (large blotches), 32282-32291, 34971-34972, Moravia de Chirripó, Limón Province (elevation *circa* 2300 ft.).

FIG. 13. *Hyla pseudopuma* Günther. KUMNH No. 37030 ♀, Moravia de Chirripó, Limón Province, C. R. Actual snout-vent length, 44 mm.

FIG. 14. *Hyla pseudopuma* Günther. KUMNH No. 32281 ♀, Moravia de Chirripó, Limón Province, C. R. Actual snout-vent length, 40 mm.

Hyla legleri sp. nov.

(Figs. 15-16)

Type: KUMNH No. 32982 ♂; collected approximately 15 km., WSW San Isidro del General, San José Province, at night with paratypes, in a small swamp, July 10, 1952, by Edward H. Taylor.

Paratypes: KUMNH Nos. 32981, 32983-32992 all males, same data. No. 35171, female same data; all topotypes collected by Edward H. Taylor and John Baker.

Diagnosis: A red-eyed species with a maximum known snout-vent length for males of 34, of female 36 millimeters; inner fingers less than one-fourth webbed; outer fingers approximately one-third webbed; toes nearly four-fifths webbed; tarsal fold not or but faintly indicated; male with vocal sac and paired vocal slits; vo-

merine teeth in two separated groups between choanae; interorbital distance greater than width of an eyelid; heel to anterior edge of orbit; venter, chin, and breast granular; tympanum about equal to area of largest finger disc; blackish to dark brown above with or without indistinct mottling; on sides the color often limited by a distinct yellow line from upper arm, along side, to groin; a cream

FIG. 15. *Hyla legleri* sp. nov. KUMNH No. 32983 ♂. 15 km. WSW San Isidro del General, San José Province, C. R. Actual snout-vent length, 33 mm.

line above vent and across heel; a fold above tympanum obscures its upper border.

Description of type: A slight depression on the snout behind level of nostrils to level of eyes; head wider than body, its width at tympanum (11.6 mm.) nearly equal to its length (12 mm.); length of eye-opening (3.4) about equal to distance between eye and nostril; latter a little closer to median point on lip than to eye; interorbital

space (4 mm.) greater than width of an eyelid (3.2 mm.); greatest diameter of tympanum (1.9 mm.) approximately equal to distance from eye; canthus rostralis distinct, rather sharp, curving slightly, the loreal region shallowly concave sloping broadly to lip.

Vomerine teeth on two low transverse ridges between choanae, separated from each other by a smaller distance than from choanae; choanae rather small not larger than vomerine tooth-groups; opening of palatal glands in a slightly sinuous transverse groove, much closer to front of palate than to upper level of choanae; tongue about as long as broad (6.5 mm.); a slight posterior notch indicated; vocal slits nearly parallel; vocal sac indicated externally by a transverse fold on throat in front of breast.

Arm rather short, thick, and cannot be straightened without breaking muscles; first finger distinctly shorter than second, with numerous brown spiny rugosities forming a broadly triangular area reaching to terminal pad; terminal pads of digits widened, those of three outer fingers much larger than that of first; first two fingers less than one-fourth webbed; three outer fingers about one-third webbed; inner metacarpal tubercle elongate; subarticular tubercles small, those on two outer fingers may be double or bifid; a slight fold on undersurface of forearm; toes about four-fifths webbed; inner metatarsal tubercle moderate, somewhat elevated; outer tubercle very small, indistinct; pads on toes smaller than those on three outer fingers, larger than pad on inner finger; heel reaches to front of orbit; legs folded at right angles, the heels overlap three millimeters; no tarsal fold evident.

Skin almost completely smooth above, on sides of venter, and underside of thighs; less distinctly so on breast and chin; some granules, on sides of vent, the posteriormost pustular, much the largest.

Color in life: Dark blackish to blackish brown above on head and body; throat grayish white; yellowish green on venter and under thigh; heels, soles, and undersurface of toes blackish green; palms greenish yellow; a short line of cream on upper arm continued on to side of body to groin; a narrow yellowish line borders upper lip; back of thighs brownish olive; eye red; a narrow cream line above vent and across elbow and heel; tibia with indistinct darker bands.

Measurements in mm. (Type, No. 32981 ♂ and No. 35171 ♀ respectively): Snout to vent, 33, 34, 37; width of head, 11.6, 11.9,

12.4; head length, 12, 12, 12; arm, 19, 18, 22.5; leg, 45, 48.5, 56.2; tibia, 17.2, 17.1, 18.7; tarsus and foot, 23, 22.5, 26.

Variation: Some of the specimens have the venter and concealed parts lemon-yellow. The cream lateral line is uneven, sometimes broken. When preserved they are dark to blackish brown, with

FIG. 16. *Hyla legleri* sp. nov. KUMNH No. 35171 ♀, 15 km. WSW San Isidro del General, San José Province, C. R. Actual snout-vent length, 37 mm.

some black spots or flecks visible on back; indistinct bands are evident on tibia.

The female specimen No. 35171 differs very markedly in color, being fawn with a flecking of brown spots often contiguous forming indefinite spots; fingers and toes with light pigmentation appearing dirty white in preservative. The yellow line, distinct on upper arm, merges with the ventrolateral coloration; yellowish cream on under surfaces. The specimen is gravid and the eggs are visible.

Remarks: This species would appear to be related to *Hyla nigripes* Cope taken at an elevation of 5000-6000 ft. on Pico Blanco, Costa Rica.

The nostril, however, is closer to the median point on lip than to eye; the tympanum is larger, equal to one third or more of the exposed part of eye ball; the foot is about one-third rather than half-webbed; the leg is shorter, the heel reaching only to front edge of orbit rather than beyond the snout. There is usually a cream lateral line rather than white spots in a dark reticulum.

The elevation of the type locality is probably not more than 600 ft. above sea level.

The female figured looks very different from the males. However, I find no pertinent structural differences. They were taken in the same small swamp at night, in rain.

The species is named for John Legler, Curator in Charge of herpetological collections at the Kansas University Museum of Natural History, who has greatly facilitated my study there.

Hyla dulcensis sp. nov.

(Fig. 17)

Type: KUMNH No. 32168; collected, Golfito, Puntarenas Province, Costa Rica, Sept. 7, 1952 by Edward H. Taylor.

Paratypes: KUMNH Nos. 32166, 32167; collected with the type, same locality, Sept. 7 and 8, 1952 by Edward H. Taylor and John Baker.

Diagnosis: Web barely indicated between three outer fingers; webs between first and second toes attached only at the base of first toe; other toes about three-fourths webbed; tibiotarsal joint reaches to front edge of eye; a very slight axillary web; subarticular tubercles single. Bones blue (in life).

Related to Hyla *eleachroa* but differs in its somewhat larger size (40 mm. for males) smaller finger and toe discs, the obsolete canthus rostralis, the loreal region not concave, and the choanae larger.

Description of type: Head somewhat flattened, its length (14 mm.) a little greater than its width at tympanum (12.9 mm.); canthus rostralis not indicated, the loreal region sloping obliquely from top of snout to lip with no (or but the slightest) concavity; nostrils lateral, the region about them swollen, with a depression between them on top of snout; in front of nostril the line of profile

FIG. 17. Upper figure, *Hyla dulcensis* sp. nov. KUMNH No. 32168, Type; Golfito, Puntarenas Province, C. R. Actual snout-vent length, 39.5 mm.

Lower figure, *Hyla eleachroa* Cope. KUMNH No. 31804, Turrialba, Cartago Province, C. R. Actual snout-vent length, 35 mm.

curves somewhat forward then back and down to lip; snout extended beyond mouth 1.4 millimeter; length of eye opening (4 mm.) less than distance between eye and nostril (4.5 mm.); interorbital width (3 mm.) less than width of an eyelid (3.6 mm.), greater than distance between nostrils (2.6); tympanum large (2.2 high x 1.9 mm. long), separated from eye by a distance of two millimeters, its upper rim partly concealed by an ill-defined fold from eye which runs diagonally backwards and down to above arm insertion.

Vomerine teeth on two small closely approximated moundlike elevations between choanae and separated from them by a distance equal to length of one elevation, the teeth arranged in slightly diagonal lines pointing forward mesially (nearly transverse in a paratype); diameter of a choana in distance between choanae about two times (or slightly more). Openings of the vocal slits large; tongue with only a small free edge, longer than wide, not notched posteriorly; palatal glands open in a sinuous groove, much closer to anterior limit of palate than to anterior level of choanae.

Hand with a web-remnant between three outer fingers, the webs continuing somewhat as small lateral fringes or ridges; between first and second fingers only the ridges are evident; discs on fingers rather large, that on third finger as large as tympanum; subarticular tubercles large, single; inner metacarpal tubercle elongate, partly covered by the nuptial gland, which seemingly lacks horny spicules on its surface; the palmar tubercle elevated, divided mesially, the inner part a little the longer.

Legs rather short; the tibiotarsal articulation reaches the anterior edge of the eye; when legs are folded at right angles to the body the heels overlap a little more than four millimeters.

Web between first and second toes slight, attached to first in basal part only; four outer toes about three-fourths to four-fifths webbed; discs a little smaller than on fingers; inner metatarsal tubercle relatively small; the outer smaller but entirely distinct; no inner or outer tarsal fold.

Skin on dorsal surface of body and head minutely granulate or corrugate (smoother in female paratype), but nearly smooth on arms and upper parts of limbs; sides nearly smooth; skin on chin covering vocal sac much folded; a small curving fold across breast; venter strongly granulate or areolate; anterior ventral surface of thighs, and to a lesser extent the posterior surface, granulate.

Color:—In life, grayish brown on dorsal surfaces, the venter white; the throat sac and chin yellow; legs generally greenish yellow. In preservative, very light brown above, the pigment (in

chromatophores) rather evenly scattered over most of the limb surfaces (a narrow ventral area excepted), and the upper and under surfaces of hands and feet; upper lip cream with some scattered pigment.

The bones are blue or greenish blue in life but this color tends to fade after preservation.

Measurements of *Hyla dulcensis* and *Hyla eleachroa*

	H. dulcensis			*H. eleachroa*		
Number	32166	32167	32168	30340	30313	30326
Sex	♀	♂	♂	♀	♂	♂
Snout to vent	40	37	39	34	33.5	33
Head length	13.5	13.5	14	12	11.5	11
Head width	13.6	12.7	12.9	11	11	10.7
Length of eye	4	4	4	3.8	3.8	3.7
Eye to nostril	4.3	4.3	4.5	3.7	3.9	3.8
Arm	24	22	24	20	19.7	19
Leg (to vent)	61.5	60	61.4	54	52	49
Tibia	21	20.5	21	17	18	17.6
Foot and tarsus	26.6	27	28.4	24	24	23.5

Remarks: This species belongs to a hylid group having the web largely eliminated between the first two toes. Other members of this group in Costa Rica are *Hyla boulengeri, H. staufferi* and *H. eleachroa.* It is probably most closely related to *eleachroa.*

The type locality Golfito meaning "little gulf" refers to the Golfo Dulce on which the town is located. The species is named for the Gulf.

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Notes on Costa Rican Centrolenidae With Descriptions of New Forms

BY

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ABSTRACT: The Costa Rican species of this family are discussed and distributional data listed. Four species are described as new: *Cochranella chirripoi*, *Cochranella millipunctata*, *Cochranella decorata*, and *Cochranella reticulata*. A key is given. Thirteen of the species are illustrated with photographs.

INTRODUCTION

Four species of diminutive frogs taken since the preparation of my paper "A Review of the Frogs and Toads of Costa Rica" are referred to the family Centrolenidae. Seemingly they are new and are described herein. In order to facilitate identification of these and other species of this difficult group, I append a brief key to the Costa Rican centrolenids and list such distributional data for the members of this family as are presented by the material in my collections.

The Costa Rican species of the Centrolenidae have the following characteristics in common: The astragalus and calcaneum are fused into a single slender element; the eyes are large, usually protruding beyond the edge of the mouth and directed forward to a greater or lesser extent; the head is usually but perhaps not invariably wider than the body. The usual dorsal coloration in life is some shade of green, but in preservative the chromataphores become lavender (magenta to purplish). In the dentate species this pigment is seemingly less soluble in preservatives than in the species lacking vomerine teeth. In certain forms, and more especially so in males, the forearm is much widened in comparison with the upper arm, and the musculature tends to prevent the straightening of the member unless the muscles or tendons are torn. In life the

arms seem to be less flexed permanently. In many of the species the skin and musculature of the venter, often also of back and limbs, are so transparent that the viscera and bones may be seen through the flesh.

Several species have the eyeball surrounded by a creamy or whitish membrane which may be seen through the skin of the upper eyelid or seen from within the mouth. In others the eyeball is black. In *Cochranella chirripoi* there was seemingly some variation as if this tunic might be retracted to some extent. This I cannot determine. In many species much of the intestine has a cream-white covering.

After a specimen has been preserved for some time the brain often can be seen with considerable clarity and certain muscles will appear different in color from other muscles, thus suggesting a color pattern.

All of the species have the terminal phalanx of the digits Y-shaped, T-shaped, or straight, and the variation may occur on different digits of the same specimen. They are never clawlike as in the Hylidae, but there is an intercalated cartilage between the two terminal bones of the digits (as is true of the Hylidae and certain other arboreal frogs).

KEY TO COSTA RICAN CENTROLENIDAE
(based on preserved specimens)

1. Vomerine teeth present. In preservatives, considerable diffuse lavender pigment (magenta to purple) giving specimens a general lavender color 2
   Vomerine teeth absent. Lavender pigment tending to dissolve in preservatives leaving specimens without pigment (except in eye), 6
2. A bony process on humerus in males (rarely visible in certain females); part of lavender pigment tends to form small punctate spots (often absent); 28 mm. ..... *Centrolene prosoblepon*
   No bony process on humerus visible externally 3
3. A pollex rudiment, in males bearing a sharp spine; 20 mm., *Teratohyla spinosa*
   No pollex rudiment, bearing a sharp spine in males.
4. Skin smooth on dorsum; no web-remnant between first two fingers; outer fingers four-fifths webbed; dorsum with minute lavender flecks and fine scattered white punctations; toes entirely webbed; 24 mm. ..... *Cochranella pulverata*
   Skin more or less distinctly granular on dorsum; size larger 5
5. Dorsum dark lavender above enclosing discrete rounded cream-white spots; this color also on upper part of thighs, tibia, and tarsus, where the cream spots are larger; legs slender, elongate; terminal

pads rather widened; eyes very large, head wider than body; interorbital distance less than width of an eyelid; 29.5 mm.,
Cochranella albomaculata

Dorsum light lavender with numerous (40-50) dark rounded lavender spots, absent on arms, thighs, and tarsus; present on tibia; interorbital distance much greater than width of an eyelid; terminal pads on fingers widened; dorsal granules stronger; 30.2 mm.,
Cochranella granulosa

6. Tympanum concealed; areas about nostrils flattened, not swollen or inflated 7

Tympanum visible though covered with a thin pigmented skin; areas about nostrils swollen; the snout, sometimes nostrils, extending beyond mouth level 10

7. A pair of discrete folds, lateral to vent, run diagonally back and down on thigh ..... *Cochranella decorata*

No pair of distinct folds in region of vent 8

8. Terminal digital pads enlarged, rounded, distinctly wider than adjoining part of digit; a white eye tunic, 23.8 mm.,
Cochranella millepunctata

Terminal digital pads truncate or subtruncate, not or only a little wider than adjoining part of digit 9

9. A distinctive white eye tunic, visible through upper eyelid as a white spot; 25 mm. ..... *Cochranella fleischmanni*

A black eye tunic, the upper eyelid appearing dark; hand proportionally larger; 24 mm. ..... *Cochranella chrysops*

10. Web between second and third fingers equally as extensive as that between third and fourth. Usually a white eye tunic; 25 mm.,
Cochranella chirripoi

Web between second and third fingers not as extensive as that between third and fourth 11

11. A coarse reticulation of lavender enclosing irregular light areas on dorsum and limbs; nostril area moderately inflated, not extended quite to level of mouth; eye tunic dark; tympanum large, directed upward; a strong tarsal fold, and a strong fold from wrist to elbow; most subarticular tubercles double; 25 mm. *Cochranella reticulata*

No coarse reticulation enclosing light areas; area about nostrils somewhat more inflated 12

12. Interorbital distance double width of eyelid; visible part of tympanum one sixth of eye length; nostrils protruding beyond level of mouth; tibiotarsal articulation reaches tip of snout; no pigment on thighs; 22 mm. ..... *Cochranella valerioi*

Interorbital distance not twice width of eyelid; tympanum larger 13

13. Eye tunic white; a reticulation on dorsum tending to enclose lighter spots in vertical series; area about nostrils inflated but not extending beyond lip; tympanum directed somewhat upwards; width of eyelid in interorbital distance, twice; 22 mm.,
Cochranella talamancae

Eye tunic black, choanae relatively large, interorbital distance one-fourth greater than width of eyelid; 26 mm.,
Cochranella colymbiphyllum

TAXONOMIC TREATMENT

Centrolene prosoblepon (Boettger)

(Fig. 1)

This species, with a type locality "plantage Cairo" (La Junta) near Limón, Limón Province, Costa Rica, has a considerable range in Costa Rica and is likewise known from Panamá and Barro Colorado Island. It occurs on both Caribbean and Pacific slopes. It also has a considerable vertical range, occurring from near sea level to elevations of from 4000 to 5500 feet.

FIG. 1. *Centrolene prosoblepon* (Boettger). KUMNH No. 32932 ♀ (showing traces of the humeral processes). Turrialba, Cartago Province, C. R. Actual snout-vent length, 20 mm.

Specimens in the Kansas collection are: Pacific drainage. KUMNH Nos. 32390-93, 12-15 km. WSW of San Isidro del General, San José Province; Nos. 36874-76, Agua Buena near Cañas Gordas, 2000 + ft. elev., Puntarenas Province; Nos. 32927-32, 36877, near Sarchi, Alajuela Province.

Caribbean drainage. KUMNH Nos. 32419-38, 36873, 37016, Cinchona, southeastern slope Volcán Poás 5000-5500 ft. elev., Heredia Province; Nos. 32803-05, 32806, Los Diamantes, near Guápiles, Limón Province; Nos. 30403, 32376-81, 32926, Moravia de Chirripó, Limón Province. Nos. 32396-32416, Cariblanco, Limón Province; No. 32395 Cartago, Cartago Province; Nos. 32385-89, near Pacayas, Cartago Province; Nos. 32382-84, Santa Cruz, Cartago Province.

The lavender pigment in these, once the specimens were preserved, is practically unchanged after ten years. One female, KUMNH No. 32932, has been found showing a small humeral process, visible externally.

Teratohyla spinosa (Taylor)

(Fig. 2)

Centrolenella spinosa Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949, pp. 259-262 (type locality, Los Diamantes near Guápiles, Limón Province, Costa Rica).

Three more topotypic specimens, KUMNH Nos. 32933-35, were taken at Los Diamantes, Limón Province, within a few meters of the exact type locality, August 13, 1952. In life the colors were: "Body nearly uniform green above, yellowish on sides of head; ground color flesh; venter greenish or transparent flesh; terminal digital pads yellowish; iris dark without whitish flecks. The bones, visible through the flesh, green."

FIG. 2. *Teratohyla spinosa* (Taylor). KUMNH No. 32934 topotype, Los Diamantes, near Guápiles, Limón Province, C. R. Actual snout-vent length, 20.2 mm.

I have examined a specimen of this species from Barro Colorado Island, Canal Zone, identified as *C. pulverata.* It may be presumed that it occurs in suitable localities along the eastern lowland of Costa Rica and into Panamá.

The lavender pigment, visible after preservation (after the green color disappears), is less soluble than in many species of *Cochranella.* The types appear practically unchanged after nearly ten years of preservation.

Cochranella pulverata (Peters)

(Fig. 3)

Hyla pulverata Peters, Monatsb. Akad. Wiss. Berlin, 1873, p. 614 (type locality "Chiriqui" Panamá).

I have traced this species to the north on the Pacific slopes as far as Sarchi, Alajuela. Dunn reports the species in Colombia and Ecuador. He also reports a specimen from Turrialba, Costa Rica. I have not seen this specimen, but I suspect that this may represent the related species *Cochranella albomaculata.* I have not seen his South American specimens of *C. pulverata.*

There are five specimens in our collection: KUMNH Nos. 36871-72, 32822-23, are from Sarchi, Alajuela Province; No. 32821 from San Isidro del General, San José Province. All are dark lavender on their exposed surfaces, with minute light dots indicated. There is a line of pigment on the upperarm and on the dorsal surface of the thigh. Below, the venter and concealed parts of the limbs are clear flesh color. The digital tips are bright orange. The vomerine teeth are present in the adults and seemingly absent in the young. The two females measure 24 and 25 millimeters, snout to vent. The largest male is 23.5 millimeters.

The relationship of the species is with *Cochranella albomaculata.* In the latter the heel extends three millimeters beyond the tip of the snout and the bones are not green in preserved specimens. The species is larger (29 mm.) with the webbing on digits distinctly greater. The toes are wider, with wider terminal pads.

The lavender pigment remains practically unchanged, after preservation, in both *C. albomaculata* and *C. pulverata,* at least for some years. In life the color was "bright yellow green with maroon or rusty yellow dots. Below greenish white flesh, transparent; underside of feet and hands light yellow."

FIG. 3. *Cochranella pulverata* (Peters). Upper figure KUMNH No. 32822; actual snout-vent length 22 mm. Lower figure, KUMNH No. 32821; actual snout-vent length 24 mm. Both specimens from Sarchi, Alajuela Province, C. R.

Cochranella albomaculata (Taylor)

(Fig. 4)

Centrolenella albomaculata Taylor. Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949 (type locality, Los Diamantes, one mile south Guápiles, Limón Province, C. R.).

Four topotypic specimens, KUMNH Nos. 32824-27, were taken at Los Diamantes, near Guápiles, Limón Province, and a single female specimen, No. 32820, measuring 29.5 millimeters snout-vent

FIG. 4. *Cochranella albomaculata* (Taylor). KUMNH No. 32820. IAIA, Turrialba, Cartago Province, C. R. Actual snout-vent length, 29 mm.

length, was taken on a banana plant near a tiny stream draining a swampy area at Turrialba. Here many other specimens were heard calling from tall trees. The latter Turrialba specimen is figured, showing the details of the dorsal markings.

In life, the color was dark green above with discrete rounded greenish-yellow spots; venter transparent flesh; hands and feet

yellowish to orange yellow. Chin, and concealed part of arms and legs, pale green. The green color has changed to lavender in preservative. This form is most closely related to *Cochranella pulverata.*

Cochranella granulosa (Taylor)

(Fig. 5)

Centrolenella granulosa Taylor, Univ. Kansas Sci. Bull. vol. 33, pt. 1, Apr. 20, 1949 (type locality, Los Diamantes one mile south of Guápiles, Limón Province, C. R.).

A third specimen of this species, KUMNH No. 32808, was taken at Moravia de Chirripó, Limón Province, in 1952. It agrees with the type in all essential characters, save that in preserved specimen the dark lavender spots are larger. The specimen, a gravid female, measures 30 millimeters in snout-vent length. The ovarian eggs show some pigmentation.

The specimen was taken on a Chinese ginger plant near a small stream. Its color in life was "dorsal surfaces bright yellowish-green

FIG. 5. *Cochranella granulosa* (Taylor). KUMNH No. 32808, Moravia de Chirripó, Limón Province, C. R. Actual snout-vent length, 30 mm.

on back; the legs and concealed parts canary yellow, with tips of toes bright orange-yellow; venter transparent flesh with a greenish or yellowish wash; blackish on upper eyelids." When preserved the green disappears and the lavender pigment produces rather large dark lavender spots on a cream background.

Cochranella decorata sp. nov.

(Fig. 6)

Type: KUMNH No. 36896 ♀, collected at Hda. La Florencia, about 3 miles west of Turrialba, Cartago Province, Costa Rica, Nov., 1952, by Jack Reark.

Paratypes: KUMNH Nos. 36883, 36884, (presumably) San José, San José Province, summer 1954; Prof. Marco Tulio Pacheco, donor.

Diagnosis: A medium-sized species (maximum size known 22.8 mm. snout to vent); head wider than body, the length of eye-opening greater than the length of the snout, nearly equal to the distance of the eye from tip of snout; nostrils not reaching as far forward as edge of mouth; first finger longer than second; outer fingers about half webbed; the web between the second and third fingers one fourth of the length of second finger to pad; that between two inner fingers one fifth length of inner to its terminal pad; tibiotarsal joint reaches at least three millimeters beyond tip of snout; a prominent fold runs from sides of vent back and down on thigh; tongue not or scarcely notched behind; no vomerine teeth; no tympanum visible.

Description of type: Width of head (9 mm.) greater than body width and greater than length of head (8 mm.); width of an eyelid (1.3 mm.) twice in interorbital distance (2.6 mm.); nostrils not extending forward to level of mouth; distance between eye and nostril (1.8 mm.) nearly equal to distance between nostril and median point on upper lip (1.85 mm.); areas about nostrils not or scarcely swollen; no canthus rostralis; tympanum not visible; no supratympanic fold or only an indication of a slight thickening.

Tongue a little longer than broad, with a faint suggestion of a posterior notch; diameter of a choana (.7 mm.) in distance between choanae (1.8 mm.) about two and one-half times; palatal glands opening in a concave transverse groove between anterior edges of choanae. (Male with a subgular vocal sac, the vocal slits short terminating near edge of tongue.)

Upper arm very slender, unpigmented; forearm widened, the bones of the hand more or less visible externally; digits with terminal pads wider than the fingers; web of two outer fingers equals length of fourth finger to its terminal pad; web between second and third

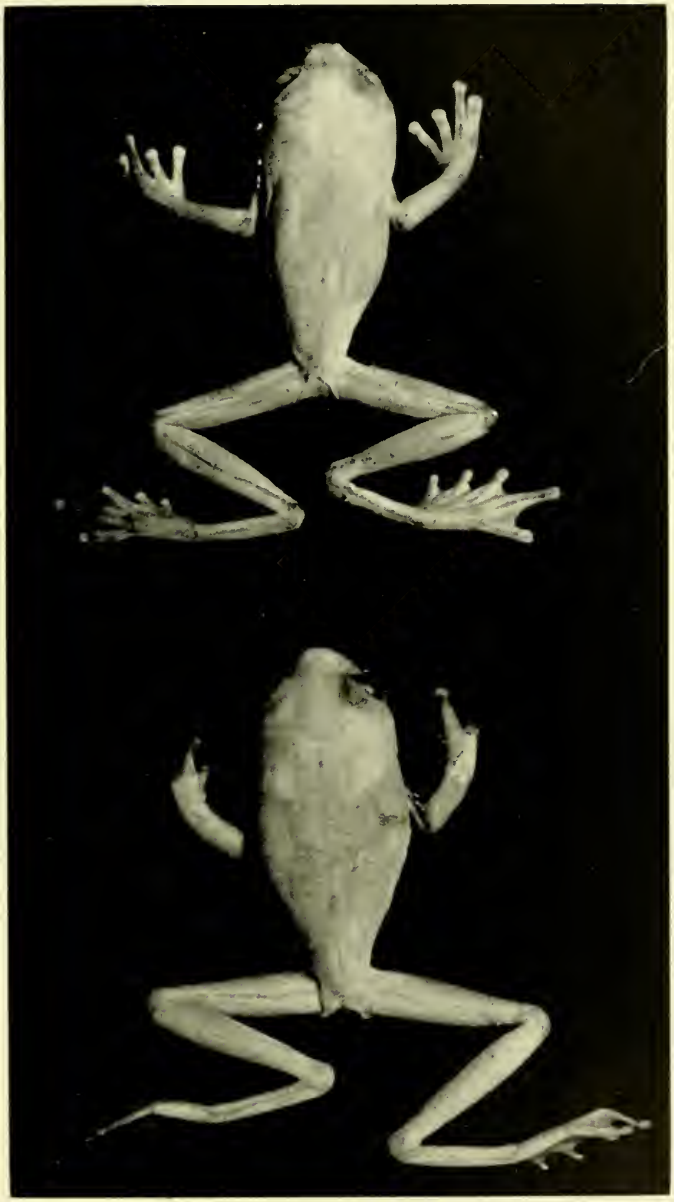

FIG. 6. *Cochranella decorata* sp. nov. Upper figure, KUMNH No. 36884, paratype, San José (?), San José Province, C. R. Actual snout-vent length, 22.5 mm. Lower figure, KUMNH No. 36896, type, Hda. La Florencia, Turrialba, Cartago Province, C. R. Actual snout-vent length, 22.8 mm.

fingers about one fourth of the length of second, with a fringe extending along edge of digit to pad, but lacking fringe on inner side of the fourth; a web-remnant between inner fingers; a flattened fold on outer side of hand and forearm. Subarticular tubercles small, distinct; a small inner metacarpal tubercle; a distinct oval or rounded palmar tubercle.

Legs elongate the heel reaching at least three millimeters beyond tip of snout; heels touch or barely overlap when folded at right angles; toes about four-fifths webbed; a slender, somewhat elongate inner metatarsal tubercle; no outer tubercle evident; a faint tarsal fold.

Skin on head smooth anteriorly, with some granules evident behind eye and at angles of the mouth; tympanum hidden under skin and muscles; under a lens dorsum shows obsolete granulation, as does upper surface of femur, tibia, and tarsus; venter and side granular, the venter tending to show transverse wrinkling; about half of undersurface of thigh smooth; posterior half somewhat granular or areolate; a strong skinfold running back and down on thigh, the anal flap somewhat thickened more or less connecting the two folds.

Color: In life, greenish above, with pale cream spots; transparent flesh below and on concealed surfaces of limbs. In preservation, at first, the green disappears leaving the ground-color yellowish white with small punctations of dark lavender. These too have now disappeared, leaving the dorsum unicolor.

Measurements in mm. (of type, No. 36384, and 36383 respectively): Snout to vent, 22.8, 22.5, 22.5; width of head, 9, 8.8, 8.9; length of head, 8, 7.5, 7.6; arm length, 14.8, 14, 14.2; leg, 39, 34, 35; tibia, 12.8, 11.4, 13; foot and tarsus 17.5, 16, 17.2.

Variation: The paratypes (not seen in life) in preservation have a scattering of lavender dots over body and the exposed parts of limbs. The skin on the dorsum of the paratypes is smoother than in the type and much of the femur is glassy smooth while the granulation is almost completely obsolete. The webbing on the hand is a trifle less than in the type. The donor of these specimens obtained them from his students. He believed them to have been taken at San José, San José Province.

Remarks: The character of the folds in the region of the vent separates this form from other known centrolenids of Costa Rica. A similar decoration appears on *Cochranella lutzorum* Taylor and Cochran, from Petropolis, Rio de Janeiro. In life there were orange

spots visible within the mouth on the palate, about the internal nares.

The type was taken from a leaf of Chinese ginger growing near a small fast-flowing stream.

The specific name is derived from the Latin *decoratus* = ornamented or decorated, referring to the folds about vent.

Cochranella millepunctata sp. nov.

(Fig. 7)

Type: KUMNH No. 36887: collected at La Palma, San José Province, Costa Rica, June 20, 1954 by Edward H. Taylor.

Paratypes: KUMNH Nos. 36883-86; 36888-94, topotypes, same data; No. 36897 Sarchi, Alajuela Province; No. 23943, (?) Moravia de Chirripo, Cartago Province.

Diagnosis: A small species, maximum size (♀) 23.8 mm.; nostrils not reaching forward to level of mouth, the areas surrounding them not elevated or swollen; front profile of snout nearly vertical, tympanum hidden; eye with a white tunic; no vomerine teeth; vocal sac present in males; terminal pads widened, distinctly wider than digits and rounded anteriorly rather than truncate; wide anal flap, the granules below vent "frosted" white; interorbital distance a fifth wider than width of an eyelid; legs folded the heels fail to meet; the tibiotarsal articulation brought forward reaches to tip of snout or slightly beyond; dorsum and head closely granular, the granules visible to eye; sides finely granular; lateral parts of venter granular, the median area vaguely so; toes about three-fourths webbed; outer fingers two-thirds webbed; less than one-fourth webbed between second and third fingers.

Description of type: Head a little broader than body; width of head (8.6 mm.) greater than length (7.3 mm.); eyes relatively small, moderately elevated, directed forward, the length of eye-opening less than its distance to tip of snout, longer than its distance from nostril; front of snout a rounded oval; nostril a little nearer mid-point on lip than to eye; no canthus rostralis; length of snout from front level of eye, two millimeters on mid-line; only a vague trace of a supratympanic fold.

Tongue (distorted in type) normally about as long as broad, free behind and on sides for about one seventh of its length; (male with vocal slits); choanae small, circular; diameter of choanae contained in distance between choanae about four times; openings of Eustachian tubes equal to or a little smaller than choanae.

Arm well developed, the fingers relatively short, the terminal pads widened, that of third finger largest (1.4 mm.) distinctly

wider than smallest width of digit (.9), the pads transversely oval; web between two outer fingers half length of fourth finger; between second and third, web about one fifth length of second finger; no web between the first and second fingers; first finger a little longer than second; fingers with slight lateral fringes except inner side of the third; a slight fold from base of first finger to elbow; no pigment on upper arm; forearm much widened at base; a small outer metacarpal tubercle; an oval palmar tubercle.

Leg long, the tibiotarsal articulation reaching two millimeters beyond snout; when legs are folded, heels touch and overlap (.5 mm.); toes two-thirds to three-fourths webbed, the terminal pads somewhat widened, the largest about as wide as that on first finger, smaller than pads on others; a small, slightly projecting metatarsal tubercle; subarticular tubercles of hand small, none double or bifid; those on toes a little smaller.

Skin above nearly smooth (under a lens very dimly granular on head, body and forearm); chin and breast smooth; venter with flat somewhat indistinct granules, more distinct laterally, obsolete on most of underside of thighs; anal flap wide transversely; vent followed by a quadrangular area of tubercles, frosted white; no anal folds.

Color in life: Above generally bluish green, with extremely numerous flecks of silvery white; eyeball with a white tunic; iris of eye whitish to golden, with numerous lavender flecks about rim; pupil longitudinal, with considerable purple flecking around it. Venter transparent flesh, the tips of the toes orange. Intestines, visible through flesh, cream-white; a whitish covering also below the pericardial cavity. In preservation, the green disappears leaving a fine reticulation of lavender or magenta enclosing small white dots, much larger than the minute "frosted" white flecks seen in life.

Measurements in mm.: (type, No. 36895 largest male, and No. 36897 largest female, respectively): Snout to vent, 21.4, 21.5, 23.8; head width, 8.5, 8.8, 9.2; head length, 7.3, 7.2, 8; arm, 16, 15.5, 14.6; leg, 38.2, 37.5, 37; tibia, 12.3, 12, 12; foot and tarsus, 16.2, 16.3, 16.1.

Variation: There is but little variation in the specimens from La Palma. The specimen from Sarchi has a slightly wider head, slightly shorter limbs, and the webs between the toes are less excised. This specimen agrees with the type in coloration.

The type locality of *Cochranella valerioi* (Dunn) is likewise La Palma, San José Province. The two forms may be readily distinguished by color markings, *valerioi* having a green median stripe;

FIG. 7. *Cochranella millipunctata* sp. nov. Upper figure, KUMNH No. 36886, actual snout-vent length, 20 mm. Lower figure, KUMNH No. 36887, type; actual snout-vent length, 21.4 mm. Both specimens from La Palma, San José Province, C. R.

in the latter the area about the nostrils much swollen and protruding, the snout and nostrils actually projecting in front of mouth; a small tympanum is visible, and there is more webbing on hand. *Cochranella fleischmanni* is also known from La Palma. This species is larger with a white spot on the upper eyelid.

The transforming tadpoles of this species were taken with the types. One specimen, with tail completely absorbed, measures 13 mm. This was taken together with other tadpoles, some having tails three or four millimeters in length.

The specific name is derived from the Latin, *mille* = thousand, and *punctum* = small dot or spot; meaning, "thousand spotted."

Cochranella fleischmanni (Boettger)

(Fig. 8)

The type locality is San José, San José. Specimens are in the collection from the following localities: KUMNH Nos. 23807-08, 30399 Cartago, Cartago Province (Caribbean drainage); No. 36895, La Palma, San José Province, 4500 ft. elev.; Nos. 30400-02, Río Segundo, Alajuela Province (Pacific drainage).

Cochranella chrysops (Cope)

(Fig. 9)

Hylella chrysops Cope, Proc. Acad. Nat. Sci. Philadelphia, 1894, p. 196 (type locality [restricted], San José, San José Province, Costa Rica.)

Specimens of *C. chrysops* were found to be plentiful at Sarchi, Alajuela. Although formerly placed in the synonymy of *C. fleischmanni*, when directly compared with that species the two are found to be distinctly different; their ranges overlap a considerable extent on the Meseta Central of Costa Rica.

This form differs from *fleischmanni* in lacking a white eye tunic (and the "white spot" on upper eyelid); in having distinctly larger hands and wider digits; the first toe is shorter, the first and second being of equal length; the head is more distinctly set off from the body.

The largest male taken measures 24 millimeters in snout-vent length. The smallest fully transformed specimen was 9.2 millimeters in length.

The following localities are represented: KUMNH Nos. 32943-55, 32962-63, 32965-66, 32968-69, near Sarchi, Alajuela Province: No. 32956 (locality uncertain); Nos. 32957-59. Cartago, Cartago Province.

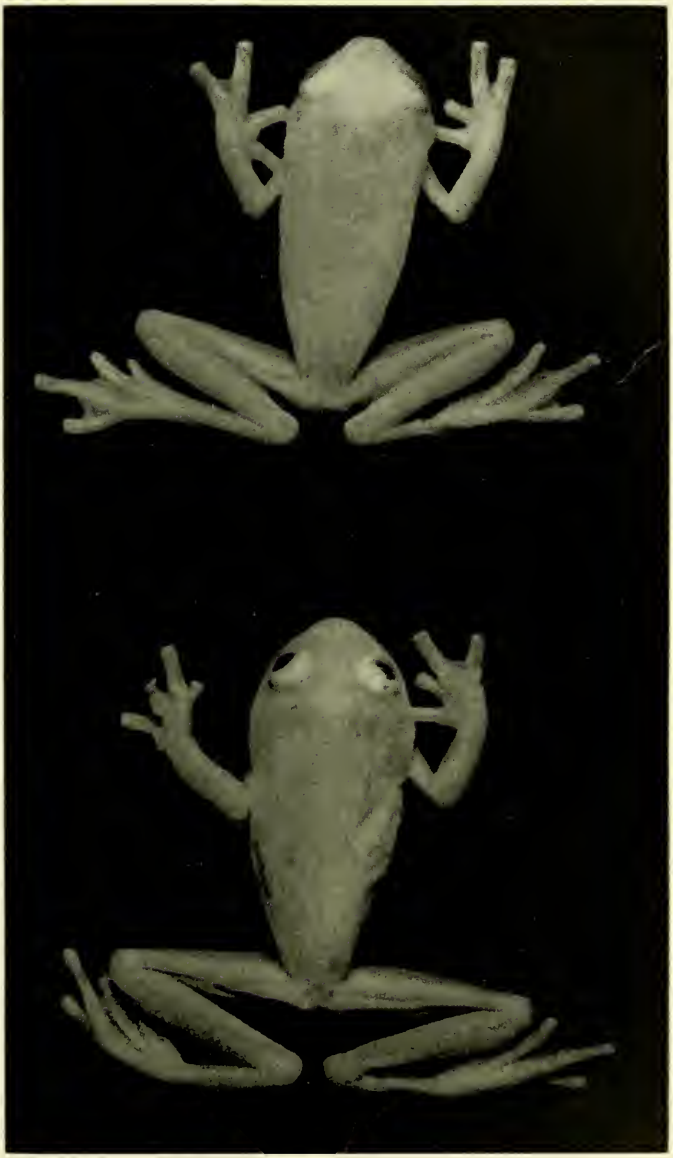

FIG. 8. *Cochranella fleischmanni* (Boettger). Upper figure, KUMNH No. 30401, actual snout-vent length, 23 mm. Lower figure, KUMNH No. 30400, actual snout-vent length, 23.8 mm. Both, Río Segundo, Alajuela Province, C. R.

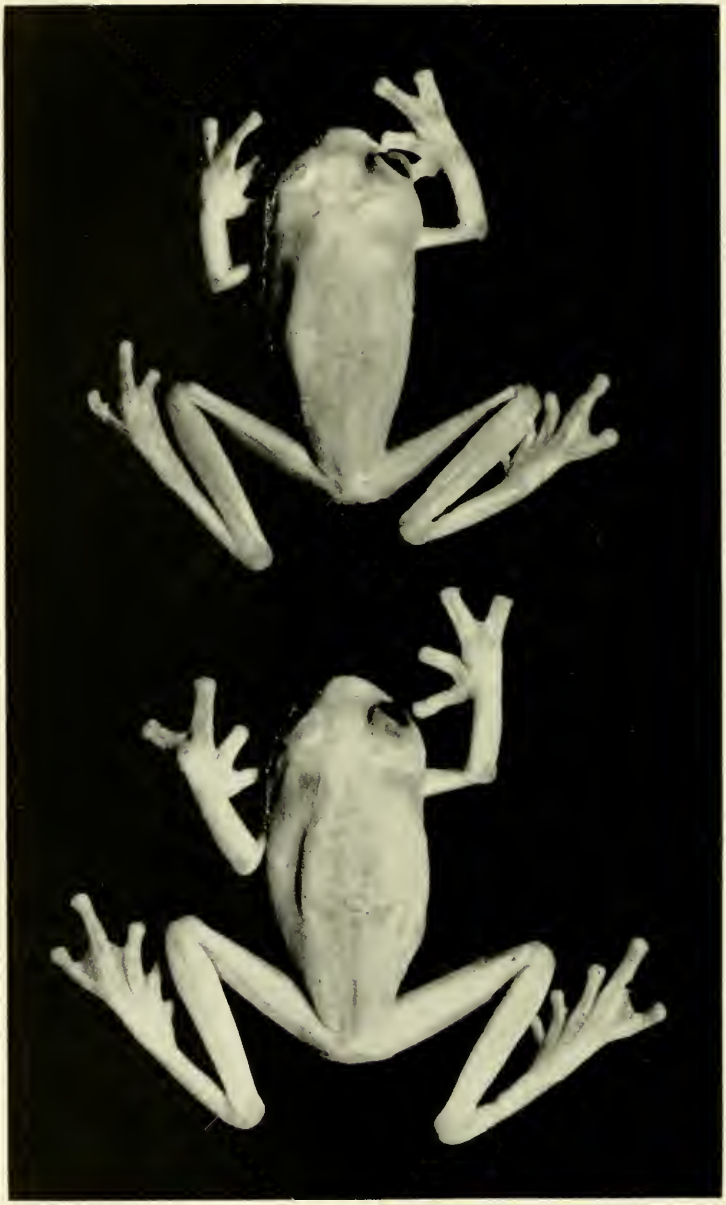

FIG. 9. *Cochranella chrysops* (Cope). Upper figure, KUMNH No. 34944, Pacayas, San José Province, C. R. Actual snout-vent length, 23 mm. Lower figure, KUMNH No. 32958, Cartago, Cartago Province, C. R. Actual snout-vent length, 24 mm.

Cochranella chirripoi sp. nov.

(Fig. 10)

Type: KUMNH No. 36865 ♀, collected on Cocales Creek, Suretka, Limón Province C. R., June 29-30, 1954, by Edward H. Taylor.

Paratypes: KUMNH Nos. 36862-64, 36866-70, topotypes, same data as type.

Diagnosis: A medium-sized species, the largest known, 26 millimeters in snout-vent length; no vomerine teeth; male with vocal sac; nostrils not extending forward beyond mouth; no canthus rostralis; tibiotarsal joint reaching two to three millimeters beyond tip of snout; heels overlap two millimeters when legs are folded at right angles to body; toes nearly fully webbed; web on hand as extensive between second and third fingers as between the third and fourth; tympanum somewhat indistinct, covered with finely granular skin; terminal digital pads on hand rather truncate, wider than narrowest part of finger. A white tunic about eyeball; skin granules distinctly visible to unaided eye.

Description of type: Head wider than body, its width (9.5 mm.) greater than its length (7.2 mm.); eye comparatively small, protruding but slightly beyond rim of mouth; no canthus rostralis; area about nostrils not or but slightly swollen or elevated (somewhat evident in certain paratypes); length of snout from front level of eyes, three millimeters; tympanum partly evident, its size uncertain, its surface covered with finely granular skin; width of eyelid (1.8 mm.) 1.55 times in interorbital distance (2.8 mm.); choanae relatively small, the diameter of one in distance between choanae, at least three times; openings of palatal glands in an undulating line, crossing palate closer to choanae than to front of palate; tongue a little wider anteriorly than posteriorly, unnotched on posterior edge, free for less than one sixth of its length; (a vocal sac present in male, the vocal slits rather far back, reaching to near the angle of the jaw).

Upper arm very slender, unpigmented, the forearm double width of upper arm; web between second and third fingers almost coextensive with that between third and fourth fingers; web between first and second finger one third length of second digit to terminal pad. The terminal digital pads one-fourth wider than narrow part of digits; outer metacarpal tubercle small; a somewhat rounded palmar tubercle; subarticular tubercles low, flattened, single; a strong fold on outer edge of hand extending to elbow.

Leg brought forward the tibiotarsal articulation reaching two millimeters beyond tip of snout; toes nearly fully webbed, the webs

FIG. 10. *Cochranella chirripoi* sp. nov. Upper figure, KUMNH No. 36865, type; actual snout-vent length, 26 mm. Lower figure, KUMNH No. 36867; actual snout-vent length, 25.7 mm. Both from Suretka, Limón Province, C. R.

reaching the terminal pads (except fourth), the webs slightly excised between toes; digital pads smaller than those on fingers; inner metatarsal tubercle distinct, somewhat elongate; outer indistinct or absent; a distinct tarsal fold.

Skin above on exposed surfaces covered with distinct granules visible to unaided eye and present also to some degree on arm; chin and breast smooth; venter strongly granular, the skin on the sides with short folds rather than granules; most of the undersurface of thigh granular; below vent an area in which the skin, covered with large granules, appears to be folded vertically; undersurface of tibia and tarsus smooth.

Color: Exposed surfaces greenish in life the color extending onto upper arm, and distinctly along upper surface of femur; distally on limbs the color reaches onto outer finger and on the two outer toes for some distance. When preserved for some time the green is replaced, and a sparse peppering of lavender or magenta dots is evident (at least so under a lens). Venter slightly yellowish flesh, transparent; digital tip orange; some pigment below vent.

Measurements in mm. (Nos. 36865, 36866, 36869 respectively): Snout-to-vent length, 26, 24, 25; width of head, 9.5, 8.5, 8.9; length of head, 7.2, 8, 8; arm length, 17, 16, 16.3; leg, 44.5, 41, 46; tibia, 14, 13, 14.5; foot and tarsus, 18.3, 17.5, 18.9.

Variation: The series of paratypes is fairly uniform save that in certain ones the white eye tunic seems to be retracted but can be seen near the base of upper eyelid; the eyeball seen from the mouth also appears dark over most of its surface.

The leg of No. 36869 is proportionally longer, the heel reaching more than three millimeters beyond the tip of the snout.

Remarks: The hands of this species have a greater amount of webbing than other species of Costa Rican centrolenids, and by this character it may be separated from the other known forms.

Specimens were discovered by following up their calls. They were found in shrubs and low branches of trees along Cocales Creek, a fast moving, shallow stream ten to fifteen feet wide.

The species is named for the local inhabitants of the area, the Chirripo Indians.

Cochranella reticulata sp. nov.

(Fig. 11)

Type: KUMNH No. 32922, collected near bridge across Río Reventazón at the Inter-American Institute of Agriculture, Turrialba, Cartago Province, Costa Rica, by Edward H. Taylor.

Paratypes: KUMNH Nos. 32921, topotype, same data; No. 32916 Moravia de Chirripó, Limón Province, June 26, 1952; Nos. 32917-20 Cariblanco,

Heredia Province, July 20, 1952; Nos. 32923-24 Palmar, Puntarenas Province, Sept. 3, 1952; No. 32925 Golfito, Puntarenas Province, September 7, 1952 (breeding); No. 36878-82 Suretka, Limón Province, June 30, 1954 (breeding).

Diagnosis: Small, maximum size ♀ 23 mm., male 22.5 mm.; greatest diameter of tympanum, about two and one-half times in length of eye; interorbital width greater than width of eyelid; no canthus rostralis; nostrils moderately prominent, nearly on a level with the anterior edge of mouth; a slight supratympanic fold not reaching eye; venter and underside of thighs granular; one-half to three-fifths webbed between two outer fingers; one-fourth, or slightly less than one-fourth webbed between second and third; only a web-remnant between inner fingers; toes about four-fifths webbed; a tarsal fold; head a little wider than body; body flesh-green above with a reticulum of deep green; eyelids deep green. The tunic of eye dark; venter and underside of limbs transparent flesh; in preservative, a reticulum formed of small groups of lavender dots.

Description of the type: Width of head, at tympanum (8 mm.) greater than length (6 mm.); eyes large, strongly elevated, protruding beyond edge of mouth; length of eye (3 mm.) greater than length of snout (2 mm.); no canthus rostralis, the loreal region not concave; area about nostrils somewhat swollen, with a slight depression anteriorly; tip of snout extending about 0.8 millimeters beyond mouth; tympanum (1.3 mm.) relatively large, contained in length of eye-opening (3.0 mm.) about two and one-half times, directed outward and upward, completely visible from above; a tiny supratympanic fold begins above tympanum and continues to above arm; interorbital width (2.2 mm.) greater than width of eyelid (1.8 mm.).

Tongue slightly free behind and slightly notched; no vomerine teeth; choanae subcircular, the diameter of one contained in interchoanal distance nearly three times; palatal glands open into a transverse groove slightly in advance of level of choanae; vocal slits opening into a large subgular vocal sac.

Upper arm very slender, unpigmented; forearm much thickened with a prominent fold from wrist to elbow; inner metacarpal tubercle elongate, scarcely elevated; median palmar tubercle rounded, rather prominent; outer subarticular tubercles on first, third, and fourth fingers double or bifid; other small tubercles on palm; fingers broad, not or but slightly widened at tips, terminally subtruncate. Web between two outer fingers slightly more than half of the length

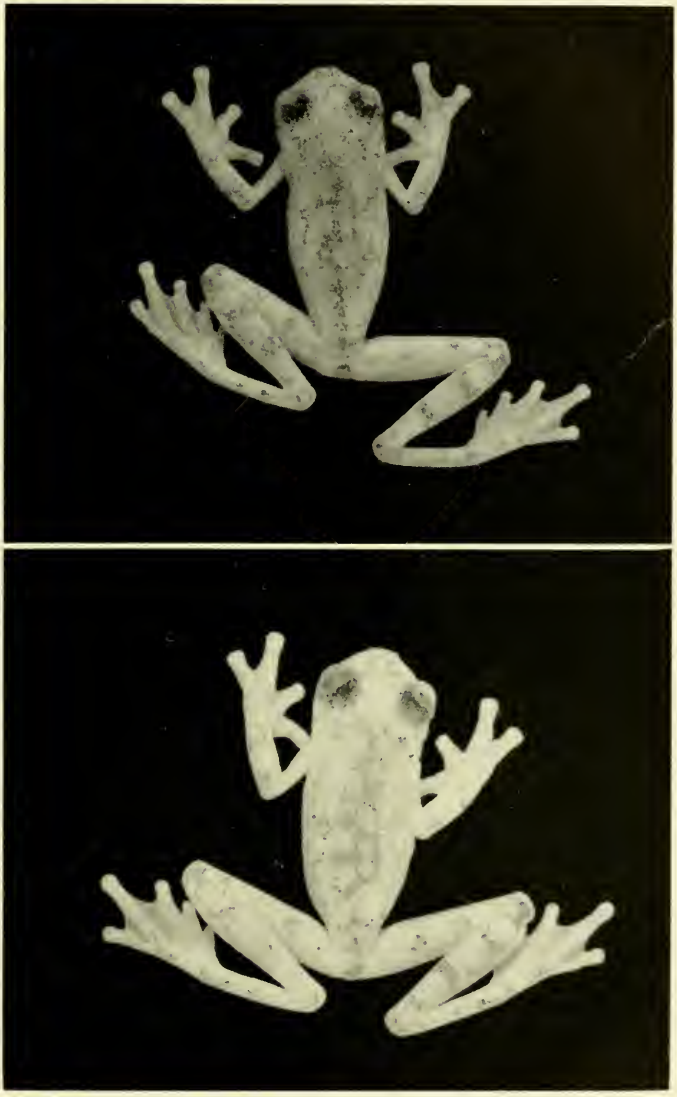

FIG. 11. *Cochranella reticulata* sp. nov. Upper figure, KUMNH No. 32921, paratype, actual snout-vent length, 23 mm. Lower figure, KUMNH No. 32922, type, actual snout-vent length, 22 mm. Both specimens from Inter-American Institute of Agriculture, Turrialba, Cartago Province, C. R.

of fourth to terminal disc; about one-fourth webbed between second and third fingers; only a remnant of web between two inner fingers; a strong fringe to disc on outer side of second and third fingers and on inner side of fourth; a slight fold on outer side of palm; first finger longer than second; subterminal pads subtriangular. Leg slender, the heel reaching the tip of snout (probably slightly beyond, normally); when legs are folded, the heels touch; toes four-fifths webbed, the web reaching to near level of the subterminal pads, except on fourth toe.

Skin above (under a lens) somewhat granular; a very shallow depression between eyes; venter and underside of thighs granular; a pair of larger rounded areolae or granules near median point under thighs.

Color: Above generally greenish flesh with a reticulation of darker green surrounding large circular cream areas; upper surface of hands and feet cream to yellowish; ventral and concealed surfaces transparent flesh. In preservative, cream-white with a reticulum composed of lavender dots surrounding rounded areas.

Measurements in mm.: Snout-to-vent length, 22; width of head, 8; length of head, 6; length of arm, 14; leg, 40; tibia, 13; foot and tarsus, 17.

Variation: The specimens of this species available show a close similarity in size between the sexes. There is practically no difference in coloration. Specimens in preservative (formalin, transferred to alcohol) tend to have the green color turn to lavender or purple which is slowly dissolved in alcohol. When this happens the color of the muscles may give the appearance of two lighter lateral stripes extending to pelvis with a very slightly darker and wider median stripe. The eyes appear black. After nearly five years in preservative the dorsal pigment marks can still be seen under a lens. The dorsal surface of thigh has scattered pigment but the hands and feet (except outer toe) are without pigment.

The tongue varies somewhat in shape in preservation, but usually it is a little wider posteriorly than anteriorly and a slight notch is indicated.

Remarks: All of the series listed are adult. Most of them were discovered by following calls, the specimens being found on the underside of leaves. Two pairs were found breeding, and in two cases single males (one the type) were observed brooding sets of

eggs under a leaf. The type was taken from a palm-tree leaf at least 25 feet above the ground. It was dislodged by a long bamboo pole. Almost directly under the eggs was a tiny rivulet flowing over rocks, entering the Rió Reventazón at a point some fifty feet away. The call is reminiscent of the call of certain local orthroptera (katydids).

Specimens taken at Cariblanco were found at night perched on smooth leaves overhanging a swift-moving irrigation canal. They were not calling. Two females, Nos. 32916 and 32923, are gravid.

Cochranella valerioi (Dunn)

Centrolene valerioi Dunn, Occ. Papers Boston Soc. Nat. Hist., vol. 5, Aug. 18, 1931, pp. 397-398. (type locality La Palma, San José Province, C. R. [4500 ft. elev.].)

No specimens of this species have been taken although search has been made in the type locality. Dunn described the species as follows:

Diagnosis: "Centrolene without humeral hooks, no vomerine teeth; tympanum almost aborted; nostrils raised prominently; bones white; color in life white with a dorsal green network.

Description: "Tongue circular; head broader than long, semicircular as seen from above save for projection made by nostrils; eyes directed forward, their diameter greater than their distance from tip of snout; canthus rostralis rounded but distinct; lores concave; nostrils protuberant, causing snout to overhang; interorbital space twice as wide as upper eyelid; tympanum barely visible, directed upward, 1/6 the diameter of eye; fingers with disks wider than tympanum, truncate; first finger longer than second; web on about ½ of outer fingers, to penultimate phalanx of 3 and 4; inner fingers webbed at base; toes webbed to just short of disks of 3 and 5, not quite to penultimate phalanx of 4; a single weak inner metatarsal tubercle; heel reaches to beyond snout; smooth above, belly and thighs rugose; in life white, a narrow green dorsal stripe, green vermiculations on dorsal surface and on shin, thigh unpigmented, white beneath, iris golden, in preservative white, a few faint dark chromatophores where green was in life; length 21 mm., width of head 8; arm 13, leg 39 mm."

I examined a specimen presumed to be a paratype, a short description of which was published by me (Univ. Kansas Sci. Bull.,

vol. 35, pt. 1, no. 5, July 1, 1952). This specimen may or may not be of the same species. I have not compared it with the type. The species appears to be related to *Cochranella talamancae* despite obvious differences. Further study is essential before the status of these two forms is fixed.

Cochranella talamancae Taylor

(Fig. 12)

Cochranella talamancae Taylor, Univ. Kansas Sci. Bull., vol. 35, pt. 1, July 1, 1952, pp. 781-783 (type locality, Moravia de Chirripó, Limón Province, C. R.).

This diminutive species (approximately 22 mm. snout-vent length) was rediscovered at the type locality, Moravia de Chirripó, Limón Province.

The following were taken: KUMNH, Nos. 30887, 32936-38 topotypes.

In life the ground color of the specimens was delicate canary yellow with a diffuse green median line joined to a fine greenish reticulation, enclosing lighter areas on dorsum. Chin bluish white, the venter transparent cream-flesh; concealed parts of limbs flesh; upper eyelid dark green over black; iris golden, powdered with deep purple; webs of hands and feet less intense yellow than on the tips of fingers and toes; on dorsal surface of legs there are slightly rounded yellow spots.

This may be the southern representative of *Cochranella valerioi* (Dunn), which appears to be its nearest relative. I have not found *C. valerioi* although I searched for it at La Palma, the type locality.

Cochranella colymbiphyllum (Taylor)

(Fig. 13)

Centrolenella colymbiphyllum Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949, pp. 262-263 (type locality, American Cinchona plantation [Isla Bonita] Volcán Poás, Heredia Province, Costa Rica).

This species is presumably confined to the northern and eastern drainage of the Cordillera Central. The following specimens, other than the types, are in the collection: KUMNH, Nos. 32939-32941 Cariblanco; No. 32942, topotype, Cinchona (Isla Bonita), both from Heredia Province.

FIG. 12. *Cochranella talamancae* Taylor. Upper figure, KUMNH No. 32937 topotype, actual snout-vent length, 21 mm. Lower figure, KUMNH No. 32938, topotype, actual snout-vent length, 21.5. Both from Moravia de Chirripó, Limón Province, C. R.

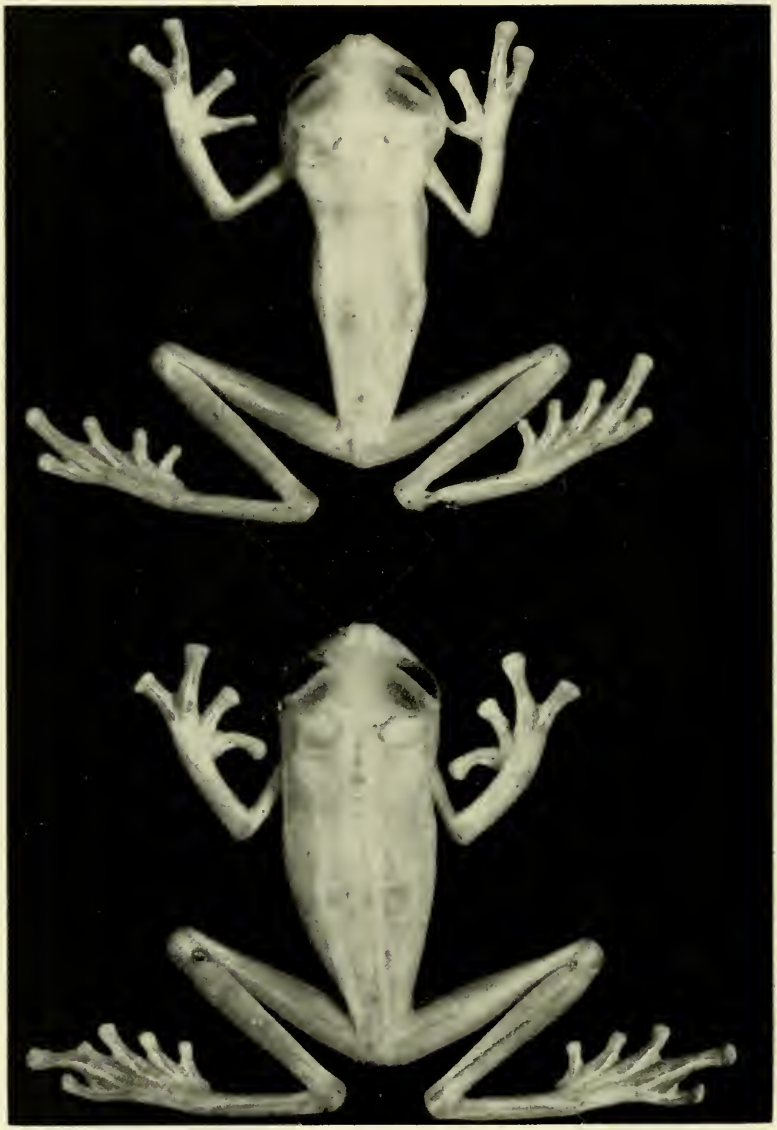

FIG. 13. *Cochranella colymbiphyllum* (Taylor). Upper figure, KUMNH No. 23812, type, actual snout-vent length, 26 mm. Lower figure, KUMNH No. 32942, topotype, actual snout-vent length, 26.2 mm. Both from Isla Bonita [= Cinchona], Heredia Province, C. R.

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Observations on the Ethology of Neotropical Anthophorine Bees (Hymenoptera: Apoidea)[1]

BY

CHARLES D. MICHENER[2] and RUDOLF B. LANGE[3]

ABSTRACT. This paper summarizes available data on the biology of neotropical anthophorine bees. It also presents new information, primarily on nesting behavior, for members of the following genera: *Paratetrapedia, Monoeca, Tetrapedia, Melitoma, Ptilothrix, Peponapis, Melissodes, Melissoptila, Thygater, Anthophora,* and *Centris.*

With few exceptions the biological characteristics of groups set forth by Linsley, MacSwain, and Smith (1955, 1956) are supported.

INTRODUCTION

This paper gives the results of a series of studies of bees of the subfamily Anthophorinae (sense of Michener, 1944) and their nests carried out principally in the State of Paraná, in southern Brasil. One purpose of this paper is to make available for comparative study the rather fragmentary data which we have gathered on the species mentioned below. Another purpose is to summarize the data now available on the biology of the nonparasitic Neotropical members of this large group of bees, with supplementary or comparative information on representatives from other regions, to provide a basis for constructive comparative work on the biology of Anthophorinae in the American tropics.

1. The preparation of this paper and the figures accompanying it was facilitated by a grant from the National Science Foundation. Thanks are due to Father J. S. Moure for identification of the South American bees concerned. We are also indebted to Prof. Domiciano Dias, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo, Piracicaba, São Paulo, Brasil, and to Mr. Alvaro Wille, Mr. Carl W. Rettenmeyer and Mr. Howell V. Daly of the University of Kansas for data which they gathered and which we have used in this study.

2. Department of Entomology, University of Kansas, Lawrence, Kansas, U. S. A. Field work for this author's part in the study was possible thanks to a John Simon Guggenheim Memorial Fellowship and aid kindly made available by the Campanha Nacional de Aperfeiçoamento de Pessoal de Nível Superior, Rio de Janeiro; the Conselho Nacional de Pesquisas, Rio de Janeiro; and the Rockefeller Foundation, New York. In particular, thanks are due to Father J. S. Moure for the use of facilities of the Secção de Zoologia, Faculdade de Filosofia, Universidade de Paraná, Curitiba, Paraná, Brasil, during a year of residence in Curitiba.

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TRIBE EXOMALOPSINI

Little has been published about the nesting habits of members of this tribe. So far as known, all nest in the ground. A tendency toward communal life exists in this group. In the species discussed below as well as in *Ancyloscelis (= Leptergatis)* (Brèthes, 1909; Jörgensen, 1912a; Michener, 1954) each female presumably makes a separate nest and indeed in *Ancyloscelis* there seems to be but one cell per burrow, but these may occur in great aggregations. Hicks (1936), however, recorded four pollen-laden females of *Exomalopsis* entering a single hole, and Dr. Paulo Nogueira-Neto of São Paulo tells us that he observed numerous females of another species of *Exomalopsis* entering a single nest. Moreover, Rozen and MacNeill (1958) surmized that various individuals of still another species were utilizing a single burrow, and they found such burrows in a large aggregation. Claude-Joseph (1926) found various individuals of *Tapinotaspis caerulea* (Friese)[1] using a single entrance hole but making separate lateral branches for cells. Linsley, MacSwain, and Smith (1954) describe how individuals of *Exomalopsis* were observed entering probably abandoned nests of other bees. Perhaps this explains how they find nests of their own species to form these common nests. A few tribal characters of the cells, based only on *Tapinotaspis*, *Paratetrapedia*, *Ancyloscelis*, and *Exomalopsis* are as follows:

Cells in series (*Tapinotaspsis* and often in *Exomalopsis*) or not (*Paratetrapedia*, *Ancyloscelis*), not separable from surrounding matrix, lined with waxlike material. Provisions in the form of a firm ball or mass of various shapes [about spherical in *Paratetrapedia* and probably in *Tapinotaspis*, elongate with a depression on one side in *Ancyloscelis* (Michener, 1954) and elongate and angulate in *Exomalopsis* (Rozen and MacNeill, 1958)], not merely packed into the bottom of the cell. Egg laid on top of provisions or, in *Ancyloscelis*, in a broad concavity along one side of an elongated mass of provisions (Michener, 1954).

Paratetrapedia oligotricha (Moure)

This is a species of the subgenus *Trigonopedia*. An enormous nest aggregation of this species was found in a vertical bank of sandy soil in Floresta de Tijuca, Rio de Janeiro, D. F., Brasil, at an altitude of 500 meters above sea level, on November 28, 1955.

1. This species is placed in a new subgenus of *Tapinotaspis*, rather than in *Exomalopsis*, by Michener and Moure (1957).

FIG. 1. Portion of a vertical bank in the Floresta de Tijuca, Rio de Janeiro, containing an aggregation of nests of *Paratetrapedia oligotricha* (Moure). The white mark at the lower right is a ruler about 11 cm. long.

There were about ten square meters densely occupied by nests (fig. 1); in one square, 10 cm. on each side, there were 41 nests. There was no evidence of old cells or nests of previous generations in this bank and Dr. Carlos Alberto Campos Seabra who took one of us to this locality had not previously seen this aggregation although he is intimately acquainted with the Floresta de Tijuca. Another bank a quarter of a mile away had been similarly densely occupied, almost certainly by this same species, three years previously according to Dr. Seabra's observations but in July, 1955,

and again in November, not a bee could be found there, only old nests with cells which contained feces and had apparently produced a crop of bees. It is clear that new aggregations can form in a brief period. Possibly additional individuals are attracted by the odor of those that have already started nesting.

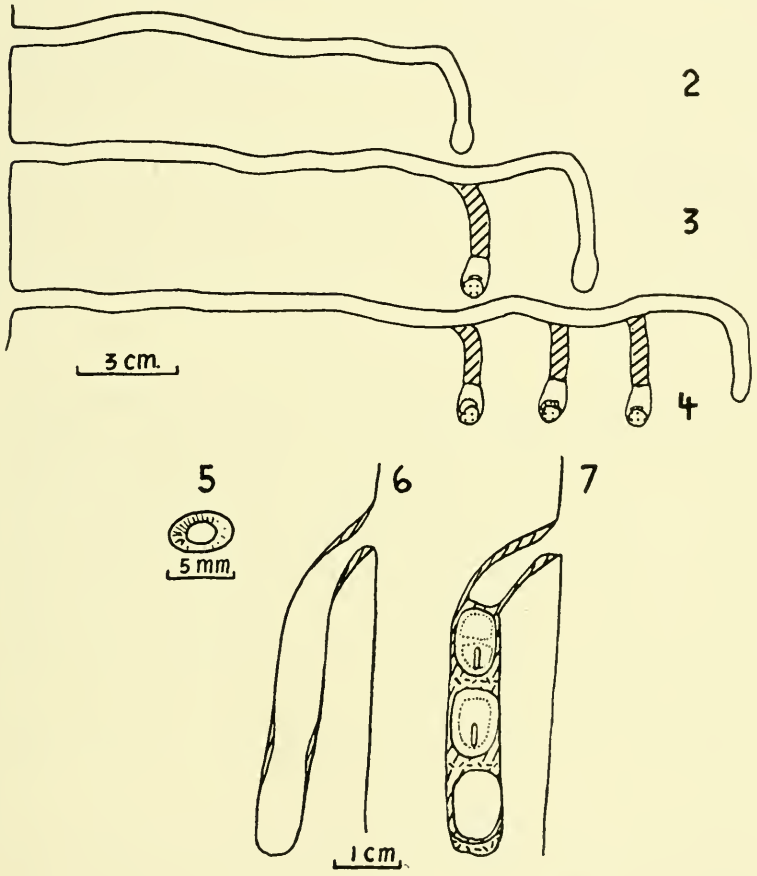
On November 28, although the bank was thick with bees in flight, some of which were starting their burrows, and the oldest larvae had not finished the last of their supplies, no males were seen. By January 9, 1956, a new generation had probably been produced, for Dr. Seabra, who visited the bank on that day, observed both sexes in flight and many pairs mating. Often pairs would roll down the bank and complete copulation at the foot of the bank. Dr. Seabra killed four pairs, taken mating, in Kahle's fixative and sent them to us. Three of the females, on later dissection showed no sperm cells in the spermatheca and therefore must have been mating for the first time when captured but the fourth already had a ball of sperms in the spermatheca. There were also sperm cells in the common oviduct. Presumably this individual must have mated previously, as the minute spermathecal entrance as well as our knowledge of the situation in *Apis* indicate that hours must be required for the entrance of a large number of sperm cells into the spermatheca. That multiple matings are not only common but the rule in *Apis* is well known (for references to pertinent literature, see Peer, 1956); it is interesting to find evidence, however fragmentary, of such behavior in other bees.

On February 22 activity of *Paratetrapedia* was continuing in the bank according to Dr. Seabra. Although there was no certain evidence that a second generation was being reared there, it is very probable. Unfortunately road construction resulted in destruction of the bank so that subsequent observations were impossible.

The same species was also observed nesting in the Bariguí roadside banks near Curitiba, Paraná, Brasil. The number, distribution and orientation of the nests, as well as climatic and soil data, are given by Michener, Lange, Bigarella, and Salamuni (1958). The nests were very few and scattered. Doubtless because of the cool climate of the south Brazilian plateau, the season of activity is somewhat different from that of the population at Rio de Janeiro. On October 17, 1955, bees were still prepupae in their cells and on March 11 and 18 nests were being constructed.

So far as known each nest is constructed by a single female bee. The nests are more or less winding, unlined, roughly horizontal

burrows 12 to 30 cm. deep, 5-6 mm. in diameter. Descending at intervals from this main burrow are vertical branches 3 to 20 mm. long, each ending in a single cell. The nest is constructed as a short horizontal burrow which turns down near the inner end and



FIGS. 2 to 4. Nests of *Trigonopedia oligotricha* (Moure) in various stages of construction. Dotted areas represent pollen balls; lined burrows are filled with earth. In left cell of fig. 3 and right of fig. 4, egg is shown on top of pollen ball.

FIG. 5. Entrance of burrow of *Tetrapedia maura* Cresson.

FIGS. 6 and 7. Nests of *Tetrapedia maura* Cresson. Fig. 6 shows burrow without cells but with gray material (lined) narrowing entrance and starting to narrow the burrow in formation of cells. Fig. 7 shows a completed nest. Short lines in various directions represent wood particles; lined area represents hard gray material brought to nests by bees. Pollen (omitted in lower cell) has dotted lines to show margins of cavities. Eggs are shown in two upper cells. (Figures 5 to 7 modified from sketches made by Alvaro Wille and Howell V. Daly.)

ends at the first cell. When this cell is complete and provisioned, the bee continues the horizontal burrow from the point where it turned downward, at the same time filling the vertical burrow, probably with newly excavated material, and soon turns down to make a second vertical burrow and cell. The process continues so that the oldest cell is consistently nearest the entrance, the youngest deepest in the bank (figs. 2 to 4). The number of cells per nest is unknown but reaches at least four. The main burrow is apparently never closed.

The vertical cells are 6 to 6.5 mm. in diameter, 11 to 12 mm. long, lined with shining waxlike material. The provisions are in the form of a rather firm ball occupying the bottom of the cell and with the gently curved egg lying on top. Some cells were found with cocoons but these were probably made by a parasite; we believe that the *Paratetrapedia* makes no cocoon.

Monoeca sp.

A single female of an unidentified and apparently new species of *Monoeca (= Fiorentinia)* was found in a nest in a tiny bare spot among grasses near São José dos Pinhais, Paraná, Brasil, February 21, 1956. The somewhat irregular burrow, with a tumulus of loose soil at the entrance, was 20 cm. deep, 6 mm. in diameter, and ended in a single vertical cell lined with waxlike material and lacking provisions. As the wing margins of the bee were entirely worn off, and her mandibles worn until they did not meet, it was obvious that this was not the first nest of this individual. Apparently *Monoeca* makes more than one nest.

Schrottky (1901) recorded that *M. schrottkyi* (Friese) made burrows over a meter deep in a bank.

Tribe Tetrapediini

This tribe was recently separated from the Exomalopsini by Michener and Moure (1957). The biological characters of the tribe, here described, strongly support this separation.

The nests are excavated in wood, the vertical cells placed in series in the burrow in the wood. The bees apparently bring in some dark substance to form the cells and to narrow the entrance to the nest. The pollen mass is firm and rather dry, vertically elongate, against one side of the cell, with a concavity which is sometimes divided by a transverse ridge. The egg is placed in a vertical position in the lower part of the concavity. This is suggestive of *Ancyloscelis* (Michener, 1954).

Tetrapedia maura Cresson

The observations recorded below were made five miles north of Guacimo, near Limón, Costa Rica, by Alvaro Wille and Howell V. Daly, both of the University of Kansas, during the period February 17 to 20, 1954. About eleven nests were found in two of the vertical supports (old, long dead trunks of small trees) of an old jungle hut. They were protected from rain by the thatch of the hut.

In dark rainy periods there was no activity of the bees. In the morning, sun struck the poles of the hut at 7:27 a.m.; the first *Tetrapedia* left their nests at 7:30. Before they left, they stood at the entrances of their nests for a few minutes, then flew off with little or no orientation flight. These bees returned in 10 to 25 minutes without pollen, but by 8:30 bees were returning with pollen. Many of the pollen-collecting trips were very short, only a few minutes long; the bees returned carrying large yellow balls of *Cucurbita* pollen on the outside of each hind tibia. In rapid flight the long legs with the pollen are folded near the under side of the body but as the bee approaches a landing they are extended conspicuously downward. Sometimes a dark material, apparently used in nest construction (see below), was carried in the scopa instead of pollen. One bee which must have been involved in excavation was seen several times backing out of its hole with large loads of wood powder. On leaving the nest it hovered and dropped dust by rubbing the legs together in flight. Sometimes a bee was seen to enter a nest backwards. Considerable confusion was noted about recognition of holes; sometimes bees attempted to enter holes much too small; one bee was seen to attempt to enter its hole, then it dragged another bee out by the leg before entering. There was no evidence, however, that more than one bee worked jointly in a single nest, although evidence obtained on opening nests seemed to indicate that a hole may be reused. After about 10:30 a. m. activity became less intense, and in the afternoon was very slight; the last bee was seen entering its nest at 5:30 p. m. Throughout the day *Coelioxys* were flying about the poles, sometimes entering holes; they may be parasites of *Tetrapedia*.

The nests consist of simple burrows which enter the wood obliquely for about a centimeter and then turn down, vertically, parallel to the surface of the pole, and extend for 3.5 to about 5 cm. (figs. 6 to 7). The burrows are oval in cross-section, 3 mm. in short diameter, 5 to 6 mm. in the long diameter. The entrance is funnel-shaped due to the placement there of a hard gray material (figs.

5 to 7) which narrows the opening. One nest opened had this material at the entrance and only a little along the walls of the burrow (fig. 6). In others the entire burrow or much of it was narrowed by similar material from which the cells were also formed (fig. 7). The cells are about 10 mm. long, 8 mm. wide, end to end in a vertical series. Their inner walls are not smooth and shining, but are made of the gray material mentioned above. All the nests that contained cells had some wood particles occupying a small space at the bottom of the nest and some had thin transverse layers of wood particles between cells. The number of cells per nest, in those that seemed to be completed, was 3 or 4. One nest already abandoned by the mother had the oblique upper part largely filled with gray solid material.

The pollen mass is unique among known bees. It is vertically elongate, about 9 mm. long and 5 mm. wide, against one wall of the cell. There is a hollow, sometimes divided by a transverse ridge, in the exposed face of the pollen mass. The egg, which is about 3.5 mm. long, is in a vertical position in the lower part of the hollow (fig. 7). The larvae apparently feed from the surface of the pollen mass, for cells with rather large larvae still have a layer of pollen adhering to the wall of the cell.

TRIBE EMPHORINI

Some of the biological characteristics of this tribe and of the genera contained in it were recently summarized by Linsley, MacSwain and Smith (1956). As always when generalizations are based on few data, as is necessary in such biological studies at the present stage of our knowledge, certain conclusions, useful at the time, prove to be premature. The following comments, then, concern additions to the valuable summaries of biological characters listed in the above mentioned work.

At least some of the South American *Ptilothrix* nest in vertical banks or in adobe walls, in contrast to North American species (see Strand, 1909; von Ihering, 1904; Ducke, 1901; and species discussed below). *P. fructifera* places its cells in series, unlike other species of the genus whose biology is known. *Diadasia chilensis* (Spinola), according to Claude-Joseph (1926), starts its turrets with the first soil excavated from the nest. This species and possibly *D. analis* (Vachal) (Bertoni, 1925), and also some *Ptilothrix* seem fully as gregarious as *Melitoma* (Strand, 1909; von Ihering, 1904; Ducke, 1901).

Among the most important characters are the form of the pollen mass, which in North American species, as shown by Linsley, MacSwain and Smith (1956) occupies the bottom of the cell and is not formed into a ball, and the position of the egg, which in these species is beneath the pollen mass. In *Diadasia baeri* (Vachal) (see Janvier, 1955) and *D. chilensis* (Spinola) (see Claude-Joseph, 1926), the egg is placed on top of a more or less spherical pollen mass, and Ruiz (1940, 1942) supports this statement in at least a general way for *D. chilensis*. In *Diadasia analis* (Vachal) also, the pollen mass is a ball, but the egg is placed at the side and beneath it, as in North American members of the genus (Janvier, 1955).

The observations reported below indicate that the egg of *Ptilothrix plumata* is on the surface of the ball-like pollen mass. As this was based on observation of a single nest it might seem to be an error. Strand (1909), however, also refers to the pollen mass of this species as a ball. Moreover, von Ihering (1904) describes the pollen mass as an oval, and states that the egg is laid after the provisioning is completed. From this we believe he meant that the egg is on top of the provisions.[1]

Tribal characters, modified from those listed by Linsley, MacSwain, and Smith (1956), are as follows: Nests usually with turrets at entrances; cells arranged serially or singly, urn-shaped, the walls constructed by the bee so that in some genera (*Melitoma*) the cells are easily separable from the matrix; waxlike linings of cells exceedingly thin or perhaps absent; cell cap not lined with waxlike material. Provisions a firm mass usually filling lower part of cell, sometimes ball-like. Egg usually below mass of provisions, sometimes on top of it. Feces (or unused pollen) spread as a layer over entire inner surface of cell, no separate pellets visible in this layer but may be visible at top of cell. Cocoon very thin.

Melitoma euglossoides Lepeletier and Serville

This species has been seen by one of us (C. D. M.) nesting in large aggregations in banks near Yautepec, Morelos, Mexico and in adobe walls near Lima, Perú, and has been recorded nesting in sim-

1. On reading the manuscript of this paper, Dr. E. G. Linsley of the University of California made some comments that seem important in this connection. He notes that he and his associates have repeatedly observed partial pollen masses of *Diadasia* and *Ptilothrix* in cells which were being provisioned. An egg was never present until the pollen mass was completed. This indicates that the egg is laid in its position beneath or at the side of the pollen mass after the mass is completed. Thus von Ihering's statement that the egg is laid after provisioning is complete may not mean that the egg is on top of the pollen. Moreover, Dr. Linsley suggests that a point of this type is very subject to observational error since pollen balls readily shake loose during excavation by an observer. It would be desirable to restudy the position of the egg in the South American species that are reported to place their eggs on top of the pollen masses.

ilar aggregations by Bertoni (1918, 1929). Moreover, the closely related *Melitoma taurea* (Say) of the United States nests in aggregations (Rau, 1929). It is therefore of interest that we found no dense aggregations of *M. euglossoides* in Brasil, but only a few nests, sometimes entirely isolated. Rau also noticed similar scattered nests for *M. taurea* in the United States and assumed that they were in unsatisfactory locations where high mortality due to lack of shelter of the bank prevented establishment of aggregations. Doello-Jurado (1912) in Argentina recorded not only an isolated nest of *M. euglossoides* but a cluster of about 25 nests in an area of four square feet in a large bank. Most of our observations were made in the Bariguí roadside banks where, as noted by Michener, Lange, Bigarella, and Salamuni (1958), this bee nests in two small, especially hard areas of the generally hard dry-looking soil of layer B, which is scarcely used by other bees of the region. In these two areas a total of 16 nests were found; sometimes two or three were close together but most were half a meter from their nearest neighbors. As *Ipomoea* flowers, on which these bees are largely dependent, are not common in the vicinity, lack of food may be the factor that limits population growth. In this connection, it is interesting to note that this bee visits flowers of cotton in large numbers near Lima, Perú.

During the season of adult activity the nests usually have a distinct turret, although frequent rains often destroy it. Only one nest in a protected situation had a long downcurved turret. During the rest of the year, when the adult bees are not active, the nests stand open. One such nest was excavated on September 16, 1955. The only two cells not moldy contained prepupae. Adults were seen in flight and constructing nests in late February and March, 1956. The nests are 5 or 6 cm. deep with several branches, each of which becomes completely filled with series of cells (figs. 8 and 9). Three nests excavated after the season of adult activity had 4, 8, and 12 cells each. By contrast, three nests excavated from shaded unbaked bricks in a porch foundation at Fazenda Salta, São Carlos, São Paulo, Brasil on April 1, 1956, after the season of adult activity, had only three or four cells each. At this locality Dr. Domiciano Dias observed bees actively making and provisioning cells, and other cells containing large larvae, as early as January 12, 1946. There is no evidence that more than one bee works in a single nest.

The cells are urn-shaped (fig. 10), horizontal to vertical, usually somewhat inclined, constructed of soil (as mud) in the cavity ex-

cavated by the bee so that they are readily separated from the matrix. The walls are about 1 mm. thick. The following measurements shown as means and their standard errors (with the number of cells measured indicated in parentheses) show the rather variable sizes of the cells: outside length, 15.48±.16 (18); inside length, 10.80±.17 (13); greatest outside diameter, 9.63±.13 (18); outside diameter at neck, 7.98±.15 (18); greatest inside diameter, 7.48±.11 (16); inside diameter at neck, 5.30±.10 (15). The outside of the cell is rather rough, the inside very smooth and very thinly covered with waxlike material which is not readily separable from the earth of the cell wall and does not quite reach the cell cap. The provisions, which have a yeastlike smell, are a stiff paste which occupies the lower part of the cell and covers the egg. The cell cap shows a conspicuous spiral pattern on the inner surface but the outer surface is beautifully smooth and concave, forming the base for the next cell in the series.

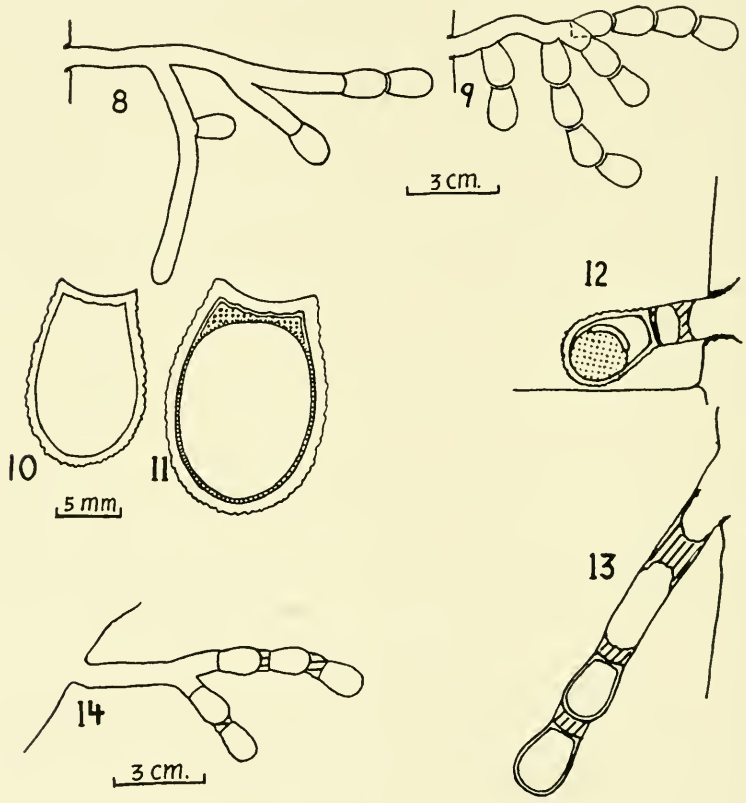
Dark feces are placed against the cell cap; the pellets are evidently soft when produced for they merge together and round out the roughness of the inner surface of the cap. A layer of white pollen .3 to .4 mm. in thickness, perhaps fecal, perhaps merely uneaten, lines the entire cavity quite uniformly, covering the dark feces. A pale brown cocoon, so thin as to be very inconspicuous, and apparently incomplete in the bottom of the cell and thickest near the cell cap, is appressed against the pollen layer. The cocoon is composed of fibers and the usual amorphous material.

Melitoma sp. ?

This species was first identified as *M. bifax* Vachal. After this paper was in press, Father J. S. Moure examined the type of that species in Paris and found it to be quite different. Our species is probably undescribed.

An aggregation of five or six nests was found in a vertical earth bank near Campo Largo, Paraná, Brasil, on January 27, 1956, by Prof. W. E. Kerr of the Universidade de São Paulo, Piracicaba. The general nest form is probably similar to that of *M. euglossoides*. There were no turrets, but the bees were not active at that time. A total of 13 cells containing living bees was excavated. Of these, two contained female pupae; five, male pupae; and six, prepupae. In the laboratory the latter did not pupate; possibly they would have remained as prepupae until the following summer. The pupae matured and all became adults by February 12.

The cells are similar to those of *M. euglossoides* in appearance but differ in some details. They differ from the description given above only as indicated below. Dimensions are as follows (based on 4 cells): outside length, 17 to 19 mm.; inside length 13.5 to 14.2 mm.; greatest outside diameter 11.7 to 13.5 mm.; outside diameter



FIGS. 8 and 9. Two nests of *Melitoma euglossoides* Lepeletier and Serville. Both were abandoned, but there is a possibility that the first was abandoned because of some mishap which befell the bee and not because she would normally have left a nest with only four cells.

FIG. 10. Longitudinal section of cell of *Melitoma euglossoides* Lepeletier and Serville.

FIG. 11. Longitudinal section of cell and cocoon of *Melitoma bifax* (Vachal). The coarsely stippled area represents feces, with a partial cocoon represented by the row of fine dots around the outside of the stippled area. The innermost line represents the cocoon proper, and the row of fine dots outside of it represents a layer of pollen.

FIGS. 12 and 13. Nests of *Ptilothrix plumata* Smith. Dotted area represents pollen mass with egg on top of it; lined areas represent earth plugs. (These diagrams were modified from drawings made by Prof. Domiciano Dias.)

FIG. 14. Nest of *Ptilothrix fructifera* (Holmberg). Shaded areas represent earth plugs between cells.

at neck, 9 to 9.8 mm.; greatest inside diameter 9.5 to 10 mm.; inside diameter at neck 6 to 7 mm. There is a thin partial cocoon, not attached to the cocoon proper, outside of the feces, obviously spun before defecation (fig. 11). The feces are whitish. The white pollen layer is thinner than in *M. euglossoides*.

Ptilothrix plumata Smith

The following observations were made by Prof. Domiciano Dias of the University of São Paulo who kindly allowed us to use material from his notebooks. The identification of the bee was made by Father J. S. Moure. The observations were made at Fazenda Salto, São Carlos, São Paulo, Brasil. The bees were nesting in a wall of incompletely baked brick. On January 12, 1946, three nests were found. One female started to dig at 1:30 p. m., worked until 5:37 making a hole 1.3 cm. deep in which she spent the night. On January 13 the bee worked all day to make the hole 2.3 cm. deep. On January 14 the single cell was completed, provisioned, and closed. The nest is diagrammed in figure 12. Some other nests contained two cells in a series (fig. 13) but obviously the bees must normally make several nests. Strand (1909) also records this species making nests containing a single cell each, although much deeper, probably because they were in a relatively soft sandy earthen bank.

During the digging process the bee makes numerous trips for water to soften the clay; after the small turret at the entrance is constructed she kicks pellets out of the hole with the legs as she digs. It was noticed that the bee enters the nest rapidly, without any wandering about or looking for the entrance.

The walls of the burrow are rather smooth but unlined. When the nest is completed, it is closed near the surface by a mud plug. The cell is roughly granular on the outside, its walls made of clay, apparently the material of the brick moistened and reworked. The inside of the cell is smooth and thinly covered with waxlike material. The cell cap shows a strong spiral pattern on the inside, is smooth and concave on the outside. The pollen is a firm mass, almost a ball, with the large curved egg (4 mm. long, .7 mm. wide) on its top surface. Von Ihering (1904) noted a coating of pollen lining old cells, showing that this species agrees with other Emphorini in this habit.

Father J. S. Moure tells us that he has seen enormous numbers of this bee nesting in a mud wall in Guarulhos, a suburb of the city of São Paulo, in February of various years, and von Ihering (1904)

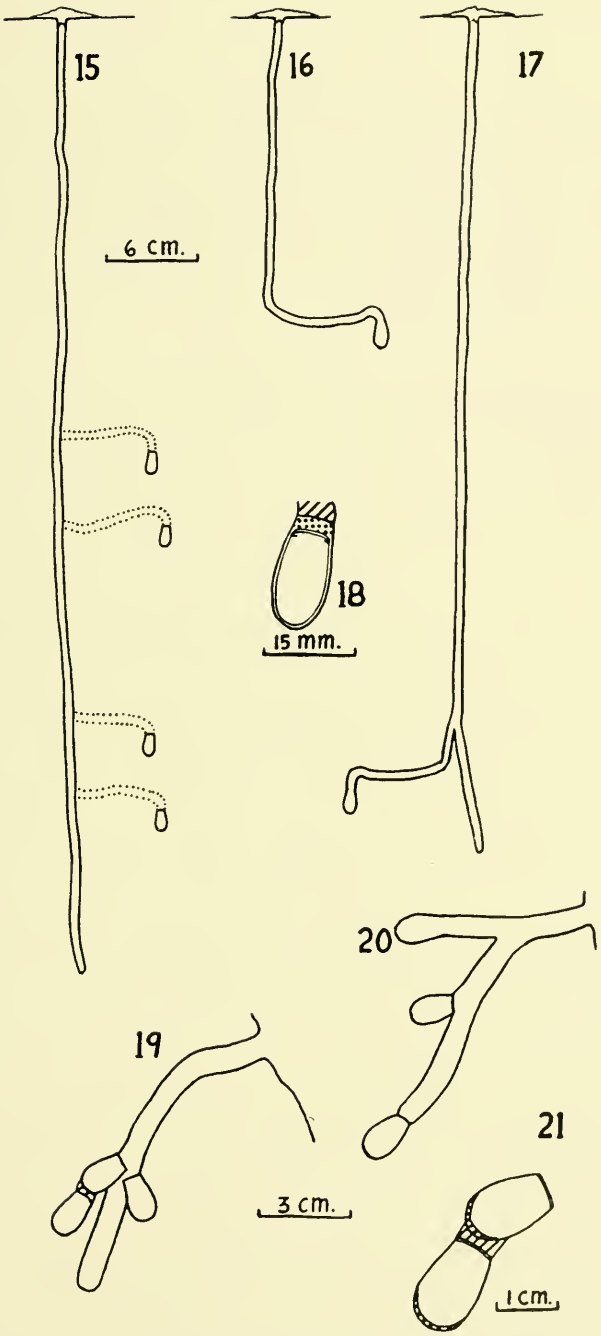
and Strand (1909) also record large aggregations of this bee in banks or termite nests.

According to Dias' description and sketch and the observations of von Ihering (1904), the nests and behavior described above agree remarkably well with those described for the North American species of the genus, *P. bombiformis* (Cresson) and *sumichrasti* (Cresson), except for (1) the shallowness of the nests, (2) the long time required to dig them in very hard material, (3) the fact that they are constructed in vertical walls, and (4) the position of the egg on top of the pollen mass. Linsley, MacSwain and Smith (1956) summarize this material for North American species and list the publications of previous authors relating to them.

Ptilothrix fructifera (Holmberg)

An abandoned nesting site was found in a subvertical bank of very hard soil along a gulley near Restinga Seca, 20 km. east of Palmeira, Paraná, Brasil, on January 27, 1956, and was excavated with the help of Dr. W. E. Kerr of Piracicaba, São Paulo. The nests were identifiable as those of this species by two living adult bees found in cells; no other living bees of any stage were present among hundreds of cells opened. The nests were so dense that their branches interdigitated, and it was with difficulty that one could be separated from its neighbors. Adjacent large areas of apparently similar banks were without nests.

The burrows, which are 9 to 10 mm. in diameter, lacked turrets, probably due to weathering, and were not plugged near the surface. They entered the bank for 4 to 9 cm., branched typically into two, although some were simple and others trifid. The cells formed series, usually of two or three, occupying nearly the entire lengths of the branch burrows (fig. 14). The general nest architecture is much more like that of *Melitoma euglossoides* than like other known *Ptilothrix*. Obviously nests were sometimes re-used, for one was found in which new cell walls had been built up in the open spaces of two previous cells. This shows clearly that the cell walls are constructed with moistened soil and are not made of soil *in situ* treated in any way. The cell walls are often more or less separable from the adjoining soil but the cells do not easily come out of the soil intact, as in *Melitoma*. The cells are vertical to nearly horizontal, the plug spirally marked on the inside, rough and not concave on the outside, thus quite unlike *Melitoma* and other *Ptilothrix*. Sometimes the cells of a series are separated by several millimeters of



Figs. 15 to 17. Nests of *Peponapis fervens* (Smith). Lateral burrows shown as dotted, leading to closed cells, were completely filled with earth and their exact positions not determined.

Fig. 18. Sectional view of cell and cocoon of *Peponapis fervens* (Smith). The dotted area represents feces; the lined area was earth filled.

Figs. 19 and 20. Nests of *Anthophora paranaensis* Holmberg.

Fig. 21. Sectional view of cell series from nest of same. Coarse dotted areas in bases of cells represent feces; lined area was earth filled.

burrow filled by loose soil; this is unlike *Melitoma* in which the cells are regularly close together. Internal cell measurements are as follows: length 12 to 15 mm.; maximum diameter 8.8 to 10 mm.; diameter of neck 6 to 7 mm. As in *Melitoma* and other *Ptilothrix*, a layer of white pollen is deposited, doubtless by the mature larva, between the thinly waxed cell surface and the very thin, brown cocoon.

TRIBE EUCERINI

Some of the biological features of this tribe were well summarized by Linsley, MacSwain, and Smith (1955[1], 1956). The study of various species unfamiliar to these authors naturally necessitates some changes in the tribal characters which they list. For example, some Eucerini, notably *Thygater analis* [also *Eucera longicornis* (Linnaeus) see Nielsen, 1941 and *Alloscirtetica gilva* (Holmberg), see Jörgensen, 1912a], nest in vertical banks as indicated below. *Thygater analis* sometimes occurs in aggregations (see Bertoni and Schrottky, 1910 and 1911, and observations recorded below), perhaps only because of limited nesting areas, but *Alloscirtetica herbsti* (Friese) nests in large aggregations (Claude-Joseph, 1926; Ruiz, 1940) as does *A. gilva* (Holmberg) (Jörgensen, 1912a), *A. tristrigata* (Spinola) (Ruiz, 1940), *Melissoptila dama* (Vachal) (Jörgensen, 1911, 1912), *Eucera notata* Lepeletier (Cros, 1939), and *E. longicornis* (Linnaeus) (Smith, 1855). Cells are single and vertical in most Eucerini, but as Claude-Joseph (1926) shows, they may be horizontal or slanting in such forms as *Alloscirtetica gayi* (Spinola) (*chilensis* Herbst) and may be end to end in modified series in this species and also in *A. tristrigata* (Spinola) and *herbsti* (Friese). These features may be characteristic of the genus *Alloscirtetica* and suggest that the "*Tetralonia* sp." found by Janvier (1955) using a nest entrance in common with *Diadasia baeri* was an *Alloscirtetica*. The three species of *Alloscirtetica* mentioned are in different subgenera. The cells are also horizontal in "*Tetralonia*" *decemcincta* Janvier (1955), a species whose correct generic position is unknown.

Much confusion has arisen from Friese's descriptions and figures of nests of *Eucera difficilis* (Dufour) (see Friese, 1919, 1923). Fortunately Höppner (1901) had given an accurate account of the nesting of this same species, indicating that the food is a paste oc-

1. In their list of genera of Eucerini, these authors were much influenced by certain errors in a previous paper of one of us (Michener, 1944). A more accurate treatment of the genera will be found in Moure and Michener (1955).

cupying the bottom of the cell, and not a ball as Friese states. The matter is further clarified, for different species of *Eucera* by Nielsen (1902), Nielson (1941) and for *Eucera* and *Tetralonia* by Iuga (1950). These authors show that in these species the food material is packed into the bottom of the cell as in other Eucerini and is not in the form of a ball. Iuga also makes clear with figures, as did Höppner verbally, the positions of the cells which were not well illustrated by Friese.

Several species of Eucerini often make nests in which two or more bees enter the same hole but probably each makes separate lateral burrows or groups of cells below the surface. This is reminiscent of the Exomalopsini and is recorded for such unrelated Eucerini as *Melissodes* sp., *Svastra (Epimelissodes) obliqua* (Say) (Custer, 1928), *Svastrides melanura* (Spinola), *Alloscirtetica tristrigata* (Spinola) (Claude-Joseph, 1926), and one nest of *Eucera longicornis* (Linnaeus) (Nielsen 1902). It probably occurs in *Melissoptila paraguayensis* (Brèthes); see below.

Tribal characters, modified from those listed by Linsley, MacSwain, and Smith (1955, 1956) are as follows: Nests (in Western Hemisphere) without turrets; cells usually arranged singly, elongate, usually vertical, with thin waxlike linings; cell cap not lined with waxlike material. Provisions a rather soft mass filling bottom of cell. Egg on top of provisions. Feces at top (cap) of cell. Cocoon thin, anterior end with multiple layers.

It is interesting that, although most Anthophorinae pass the winter as prepupae, *Eucera notala* Lepeletier metamorphoses in the fall and winters as an adult (Cros, 1939). This is contrary to the principal biological character of the subfamily brought forward by Linsley, MacSwain, and Smith (1956) to justify its elevation to family rank.

Peponapis fervens (Smith)

This is the bee that collects pollen from flowers of squash (*Cucurbita*) in the early mornings in Argentina, Uruguay, Paraguay, and southern Brasil, just as do species of *Peponapis* and *Xenoglossa* in North America. Also as in North America, *Peponapis* occurs around cultivated patches of squash (*abobora*) in regions where the plant apparently was never wild. Our observations were made at Curitiba, Paraná, Brasil, where nests were found in flat ground only a few meters from a squash patch, and at São José dos Pinhais, Paraná, Brasil, where a nest was found in flat ground 50 meters or

more from the nearest squash flowers. All excavations were made from February 16 to 21, 1956.

There was no evidence that more than one female occupied a single nest. Nests were found in the process of construction with no cells, and with larvae of all ages up to prepupae. The main burrow of each nest is vertical, very straight, 6.5 to 7.5 mm. in diameter (figs. 15 to 17). The inner walls of the burrow are very smooth but not lined with any visible material. Nests being excavated have large tumuli which completely close the entrances with loose dirt through which bees dig on entering or leaving.

Lateral burrows 4 to 7 cm. long extend at intervals from the main burrow; near their ends each turns downward and terminates in a single cell. In the only nest excavated which had several (4) such laterals and cells, the upper was the oldest. Laterals leading to closed cells are completely filled with soil and indistinguishable or nearly so. Cells were found from 20 to 60 cm. deep and one main burrow extended to a depth of 63 cm. There is evidence that a bee makes more than one nest, for a female with badly worn mandibles was found in a hole with only a single lateral and no completed cell.

Cells are vertical, 8 to 9 mm. in maximum diameter, 14 to 16 mm. long, lined with a waxlike material almost to their upper ends. They are not separable from the surrounding matrix like those of Emphorini but the soil on all sides of a cell, for a distance of 3 mm., is harder than adjacent earth as though impregnated with some material. The cell plug is rough on the inside and shows no spiral pattern.

The cocoon spun by the mature larva is thin, although thicker than in *Melitoma*, and easily pulled from the cell wall, pale brown, made of fine fibers and a brownish amorphous material. At the upper end the cap is conspicuously double and there is an inner flange or partial third layer (fig. 18). The feces, which are in the form of small fused pellets, are above the cap.

Male *Peponapis* often spend the day in closed flowers of *Cucurbita*, just as among North American species of *Peponapis* and *Xenoglossa*.

Melissodes nigroaenea (Smith)

A single nest in a nearly vertical bank near São José dos Pinhais, Paraná, Brasil, was found on February 21, 1956. It was 7.5 cm. deep and contained two cells, one provisioned and closed and the other empty. The cells were end to end (*i. e.*, in series) at the bottom of

the burrow; the provisions were a paste entirely occupying the bottom of the cell. The wing margins of the bee were entirely worn off and the mandibles were very much worn; if she produced a reasonable number of cells during her life this must have been at least her second nest.

Nests of *Melissodes sexcincta* (Lepeletier), another South American species, were described by Janvier (1955).

Melissoptila paraguayensis (Brèthes)

Two nests were found in small subvertical earth banks, one near São José dos Pinhais, Paraná, on February 21, 1956, the other in a suburb (Xaxim) of Curitiba, Paraná, Brasil, on March 12, 1956. The latter was 8 cm. deep and ended in a single vertical empty cell. The former was more interesting as it was 24 cm. deep and ended in a single vertical empty cell but contained two female bees, one in a small diverticulum near the entrance. Both bees had the wing margins entirely worn away and the mandibles much worn. They must have worked elsewhere, then joined, as senile bees, in this nest.

In another species, *M. dama* (Vachal), which, however, belongs to another subgenus, Janvier (1933) reports that each nest contains 6 to 10 cells.

Thygater analis (Lepeletier)

Aggregations of nests of this bee have been recorded previously (Bertoni and Schrottky, 1910, 1911) and one of us (R. B. L.) has studied an aggregation nesting in a small bank in the city of Curitiba. At least in this latter case, however, suitable banks were very scarce while bushes and trees of *Cassia*, a favorite food source for this bee, are abundantly planted as ornamentals; we presume that the density of nests in this case may have resulted from the small nesting space available and not from any innate aggregative tendency. In the Bariguí roadside banks, as shown by Michener, Lange, Bigarella, and Salamuni (1958), nests of this *Thygater* are widely scattered. During February and March, 1956, females of *Thygater* were often seen flying about the banks as though looking for nesting places. Special attention is characteristically given in such flights to depressions or cavities in the banks and nests are usually constructed in such depressions or beneath a small overhang. There was never any evidence of more than one bee occupying a nest.

Details of the life history of this bee will be reserved for a subsequent paper by one of us (R. B. L.). It will suffice here to note

that the main burrow is roughly horizontal although usually strongly undulating and extends from 15 to 28 cm. into the bank and that the cells are located at the terminations of burrows descending at intervals from the main burrow, one cell per branch burrow, so that the nest plan roughly resembles that of *Paratetrapedia oligotricha*, described above. The descending burrows are not really vertical but alternate, one inclined to the right, the next to the left, etc., as in nests of *Eucera* and *Tetralonia* (references under Tribe Eucerini, above). The mature larvae construct light brown cocoons and pass the winter as prepupae, pupate in the spring, and emerge as adults in summer.

The nests attributed to this species by Janvier (1955) must have belonged to a different form, for he records largely vertical burrows in flat ground ending in a palmately arranged group of five or six cells.

TRIBE ANTHOPHORINI

Some of the biological characters of the tribe Anthophorini can be summarized as follows (following the excellent account of Linsley, MacSwain and Smith, 1956):

Cells usually arranged in series (sometimes very short), urn-shaped, not separable from surrounding matrix, with thick lining of waxlike material; inside of cell cap thinly lined with waxlike material except in center. Provisions with a strong fermenting odor, semi-liquid at least at surface. Egg floating on surface of provisions. Larval feces in bottom of cell, pellets not separate. No cocoon.

The species described below agrees with other Anthophorini in the characters listed above; these features are therefore not repeated in the following account. In connection with the statement that cells are arranged in series, attention should be called to the twice trifid series described by Claude-Joseph (1926) for *Anthophora incerta* (Spinola), and to the description by Fahringer and Tölg (1912) of clusters of cells in a chamber for *A. garrula* (Rossi).

Janvier (1955) reports two or more females entering a single nest in *Anthophora incerta* Janvier (not Spinola) and *A. escomeli* Brèthes.

Anthophora paranaensis Holmberg

Nests of this bee were found isolated, never in aggregations, in banks at Araucaria, Restinga Seca, São José dos Pinhais and in the Bariguí roadside banks at Curitiba, all in Paraná, Brasil. The first nests were found on January 13, 1956, at which time some bees had already completed up to three cells while others were still un-

emerged adults in their natal cells. On January 27 two cells were found still containing white pupae; kept in the laboratory at 20° C. adults did not emerge until March 12. On February 21 and again on March 3 newly started nests were found. Probably there is but one generation per year but the time of emergence is obviously protracted. One nest excavated on January 13 contained three cells, one being provisioned, another containing a live mature female *Anthophora* still sealed in the cell and the third containing only mold. This indicates either an extremely long life for the maker of this nest, or more likely, the use of an old nest by another bee.

Nests lack turrets, the soil excavated from them merely tumbling down the bank from the nest entrance. They are most often constructed in very hard soil but one was found in a soft, rapidly eroding bank. Burrows are 5 to 10 cm. deep, 7.5 to 8 mm. in diameter, and extend inward and downward. The walls of the burrow are rough, unlined. The number of cells per nest was small in all cases, varying from 1 to 3, and the four nests examined which were constructed in late February and March had only one or two cells each. This seems to indicate that a single female makes more than one nest. Not over two cells were ever found end to end in a series. The cell position varies from nearly horizontal to nearly vertical. Cells are sometimes in the end of the main burrow, sometimes in short lateral burrows (figs. 19 and 20). Cells measured (3 in number) were 14 to 14.5 mm. long, 8.8 to 9.5 mm. in maximum width, and 6.5 mm. in width at the mouth of the cell. The latter point is clearly constricted in relation to the diameter of the burrow. The cell plug is concave on the inside, without any evident spiral or other pattern, and made of a layer of very fine soil about half a millimeter thick (fig. 21). Eggs are white, strongly curved, of uniform diameter, 3.5 mm. long, .75 mm. thick.

It is interesting that Holmberg (1903) mentioned *Coelioxys colobopty che* Holmberg as a parasite, presumably taken from the nest, of *Anthophora paranaensis*, but did not describe the nest.

Tribe Centridini

Little is known about the biology of members of this tribe. The nest locations are varied; some species of *Centris* make burrows in flat ground. Dr. W. E. Kerr of Piracicaba, São Paulo, Brasil, has reported to us the nesting of enormous numbers of *Centris aenea* Lepeletier in the flat ground about the airport at Porto Atlantida, Mato Grosso, Brasil, in July, 1954. Mr. Carl W. Rettenmeyer has ob-

served a female of *C. poecila* Lepeletier going in and out of a burrow in flat ground at San Carlos, Panamá, and Schrottky (1904) records similar nesting sites for *Centris*. Other species nest in banks or mud walls (Claude-Joseph, 1926; Bertoni, 1929; Ruiz, 1940; Vesey-FitzGerald, 1939; Jensen-Haarup, 1908; Jörgensen, 1912a; Janvier, 1955). Some do not make their own burrows but take advantage of available holes, such as those in an old *Sceliphron* nest (Vesey-FitzGerald, 1939) or old holes made in wood (Jörgensen, 1912, 1912a, and *lanipes* discussed below). Such holes are partially filled with earth, or in the case of *C. labrosa* Friese and *minuta* Moesary, with leaf fragments, in which the cells are placed.

We have not observed the carrying of materials to fill holes, but Mr. Carl W. Rettenmeyer of the University of Kansas has kindly allowed us to extract data pertaining to this matter from notes which he made on Barro Colorado Island, Panama Canal Zone. In April and May, 1952, March, 1955, and February to July, 1956 he noticed *Centris dichrootricha* Moure and *C. vittata* Lepeletier collecting mud in a bare area near the laboratory. A minimum of seventy-five females of *C. vittata* were collecting mud at this place during the six months of 1956 when he made these observations. The soil was a rather loose, sandy dirt. The bees appeared rather gregarious in their collecting. Up to four bees might be seen working in an area 20 cm. x 20 cm., although similar soil, often otherwise without bees, occupied an area of over five square meters. As many as ten bees might be in sight at the same time, arriving, leaving, and gathering dirt. The bees fly low over the area and may land several times before they start gathering soil. They visit various sections of the large area and after one bee settles, others often alight near it. The soil is carried on the scopa of the hind legs, like pollen, and Mr. Rettenmeyer has specimens in which the scopa is thickly covered with dirt. He has seen one *Centris* (possibly *dichrootricha* but not collected for identification) carry soil on the scopa into a hole in the side of one of the laboratory buildings.

Centris thoracica Lepeletier, *C. sponsa* Smith, and *C. derasa* Lepeletier have been recorded as nesting in termite nests (Silvestri, 1903; Pickel, 1928; Vesey-FitzGerald, 1939) and this seems to be the usual and perhaps only site for *C. sponsa*, according to Pickel, who remarks that the cocoons of this species are so well constructed that the termites are unable to perforate them. Various species are known to nest in large aggregations, usually in banks.

Some species of *Epicharis* also nest in banks (Vesey-FitzGerald, 1939). *E. rustica* (Olivier) was seen by that author, as was *E. ele-*

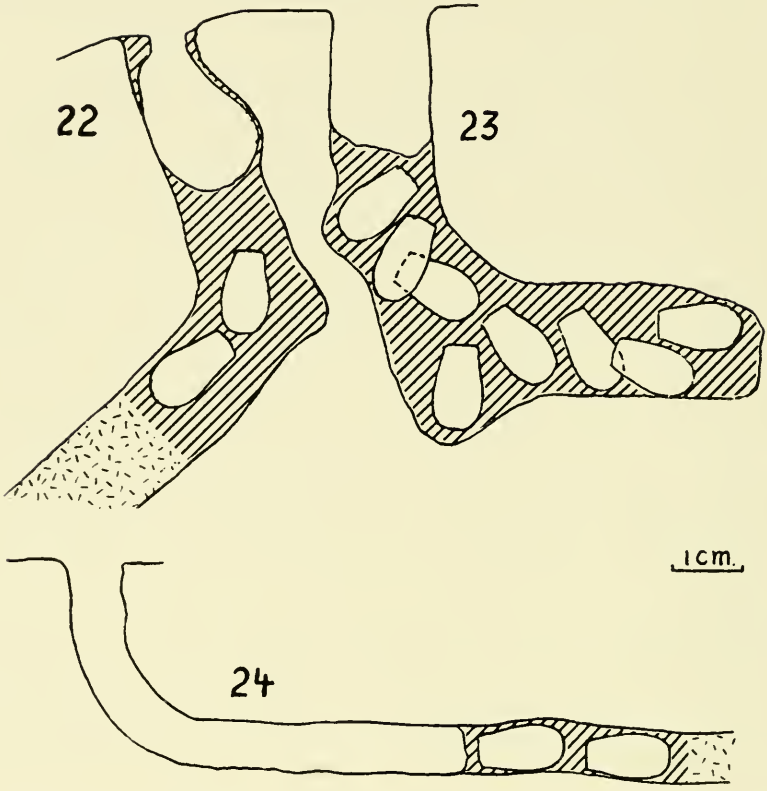
gans Smith at El Salto, San Luis Potosí, Mexico, by C. D. M., nesting in banks which were so overhung in cave and mine mouths as to be in permanent twilight.

Cells are usually arranged singly, not in series, except when (as in fig. 24), limited space forces cells into series. In *C. autrani* Vachal (Janvier, 1955), however, the cells are arranged in rather long series in burrows in earthen walls. In *C. sponsa* the cells are arranged in series of two to four; adults emerge to the side and make separate exit burrows, a behavior pattern which is not surprising since termites quickly close the original nest burrow with their nesting material (Pickel, 1928). Nests of some species have cells, one each, at the ends of very short laterals (Claude-Joseph, 1926). In *C. furcata* Fabricius the cells descend directly, without individual burrows, from the subhorizontal burrow (Janvier, 1955). The cells are elongate urn-shaped, the inner walls heavily waxed. In the two species of *Centris* discussed by Claude-Joseph the cell plugs have a hollow conical projection in the middle but this was not observed by Vesey-FitzGerald who mentions that the cell of *Centris rufosuffusa* Cockerell is closed by a disk of waxy material, and does not occur in *C. sponsa, C. autrani,* or *C. furcata.* Provisions are in the form of a paste occupying the lower half of the cell and sometimes covered with a layer of liquid. The egg is on the surface of the provisions. The cocoon is strong and in the species discussed by Claude-Joseph has a protuberance extending into the hollow projection of the cell cap.

Centris lanipes Fabricius

Bertoni (1918) mentions finding hundreds of nests of this species in the mud walls of a house, and a single nest among those of an aggregation of *Melitoma.* He says that the burrows, one for each female, penetrate horizontally or obliquely for a few centimeters. In 1929 the same author mentions large mixed colonies of these two species of bees, and mud walls completely mined over a period of years by the *Centris* burrows so that the holes intercommunicate and the cells touch one another. He also describes turrets at the nest entrances but to us it seems likely that these belonged to intermixed *Melitoma* nests since turrets are not elsewhere described for *Centris.* As there has been taxonomic confusion among relatives of *lanipes,* he may not have referred to the same species as that discussed below.

Nests of this species were found by Father J. S. Moure in old pieces of logs and in wooden buildings near the beach at Caiobá,



FIGS. 22 to 24. Nests of *Centris lanipes* (Fabricius) in holes in old wood. Frass and wood fragments in the holes are represented by short lines variously oriented; the lined areas represent sandy clay perhaps placed in the holes by the bees.

Paraná, Brasil. He kindly brought one large piece of a long dead tree containing six *Centris* nests to the laboratory in Curitiba. The journey over rough roads apparently destroyed the eggs, so that their position in the pollen mass could not be determined when the nests were opened on December 5, 1955.

The nests were all in old holes made by wood boring Coleoptera. These holes were often partially filled by frass and wood fragments evidently left there by the borer. However, the outer several centimeters were filled by sandy clay, no doubt placed there by the bees, and the cells were constructed in this earth (figs. 22 to 24). In one case (fig. 22) earth formed a plug, perforated by a hole 5.5 mm. in diameter at the entrance. In this case the large space behind the

plug gave the impression of being a cell under construction; the other cells in the nest were of recent construction as they contained no larvae; probably the bee was still bringing clay to the nest when its work was interrupted.

From two to eight cells were formed in each nest, depending partly on the size of the space available for cell construction. The cells occupy all possible positions from horizontal to vertical. They are lined with waxlike material; dimensions of the cells are as follows: length 11 to 13 mm.; maximum diameter, 6 to 7 mm.; diameter at mouth of cell, 4 to 5 mm. The provisions were semiliquid. Larvae of all sizes, but no prepupae or pupae, were found in the cells.

Jörgensen (1912) records very similar nests of *Centris nigriventris* (Burmeister) in an earth filled bamboo stem and (1912a) in abandoned insect burrows in posts.

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The Flora and Ecology of the Chautauqua Hills in Kansas

BY

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ABSTRACT. This paper reports 1030 taxa of vascular plants for the Chautauqua Hills Physiographic Province in southeastern Kansas. Species percentage composition for the characteristic plants of the woodland and prairie is included. An account is given of the original vegetation of the area at the time of settlement.

The higher plant associations of the province are considered along with descriptions of their seasonal aspects. Eleven tables, two maps, and 21 plates, made from photographs by the author, are included in this work. The vegetation of the Chautauqua Hills in Kansas is most closely related to that of the Texan Biotic Province.

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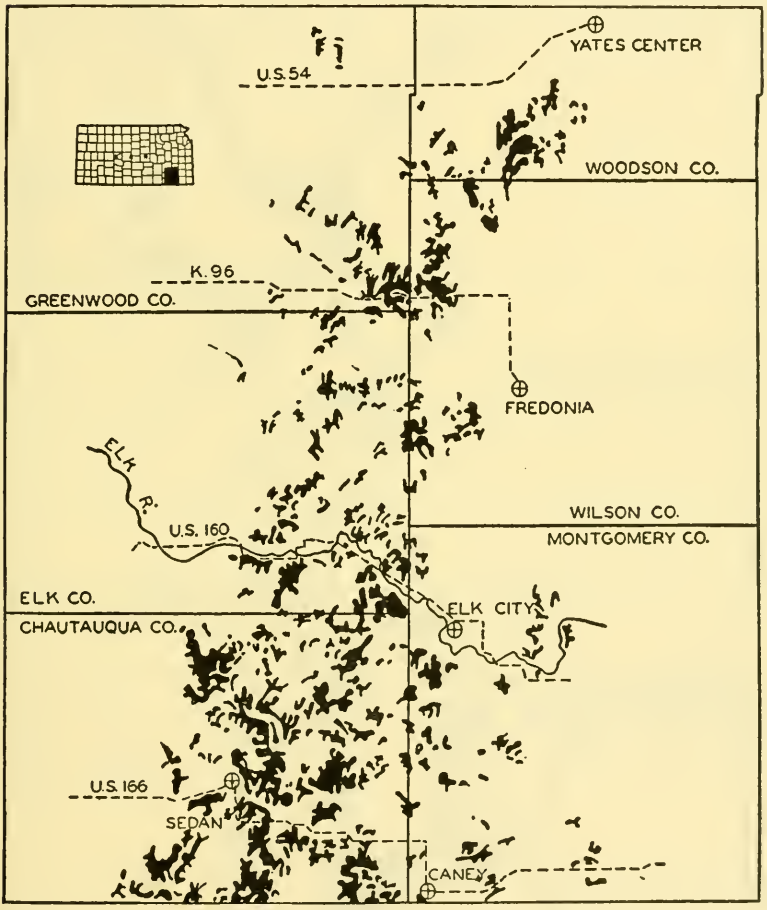
INTRODUCTION

The name Chautauqua Hills was first applied by Adams (1899) to that area lying within a triangular belt approximately ten miles wide extending from Yates Center in Woodson County, Kansas, southward to the State line in Montgomery and Chautauqua counties (Maps 1 and 2). Schoewe (1949) describes the area as follows. "The Chautauqua Hills are developed chiefly in the thick sandstone of the Douglas group which farther to the north are replaced by shales and which there, because of their position between the limestones, produce escarpments." As a result of erosion, the surface of the sandstone belt has been dissected into a series of low hills which are intersected by deep gullies which have been cut by many small streams. The Verdigris, Fall, and Elk rivers cross the area (Map 2) in low narrow valleys. In many places the rivers and valleys are bordered by bluffs which show sandstone outcrops (Plate 17).

This area is described by McGregor (1955) as being distinguished primarily by sandy soil and sandstone capped hills whose tops and upper slopes are forested (Plates 1 and 2) with *Quercus stellata, Q. marilandica, Q. velutina,* and *Q. prinoides* (Table 1) with *Q. muehlenbergia, Q. macrocarpa, Carya cordiformis, C. ovata, Ulmus americana, U. rubra,* and *Celtis occidentalis* becoming admixed with

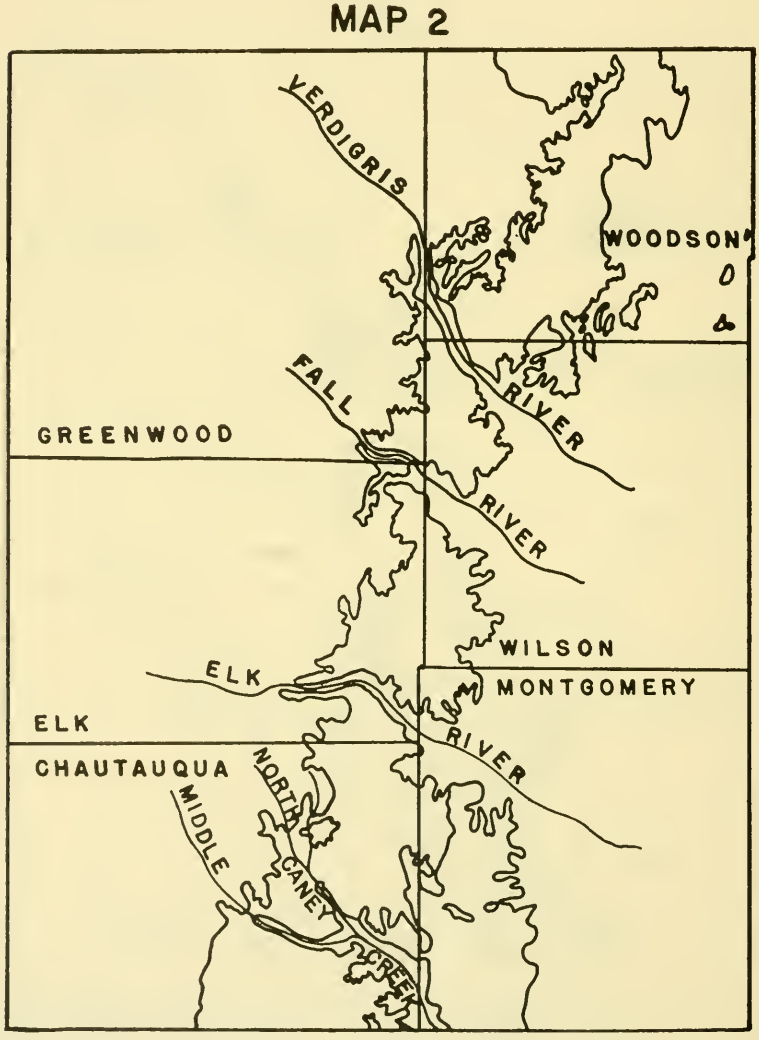
MAP 1



MAP 1. The Chautauqua Hills area showing location of upland woods and major cities and highways. Copied from Hale (1950) as taken from aerial photographs, 1954 (U. S. D. A. Commodity Stabilization Service, Index Maps, scale 1:20,000).

the above on the lower slopes and along the streams (Tables 2, 3, and 5).

Yates Center is the chief town at the north border of the Chautauqua Hills area, Toronto, Fall River, Elk River, Sedan, and Elgin mark its west border whereas Tyro, Elk City, New Albany, and Coyville define its east border.



MAP 2. Tracing from the Geologic Map of Kansas, Moore and Landes (1937), showing the area of Douglas sandstone and major stream courses of the Chautauqua Hills.

The Chautauqua Hills area is a physiographic province in Kansas. Actually it is the northern limits of the Texan Biotic Province and is bounded on the east and west by physiographic provinces, the Osage Plains and Flint Hills respectively, and on the north by the Illinoian Biotic Province. From the east there is an influx from the Carolinian and on the west from the Kansan Biotic Provinces. Thus the area is unique in that it is a unit with three boundaries which form transitions.

In addition to Schoewe (1949) and McGregor (1955) one other publication, Hale (1955), includes mention of the characteristic trees of the Chautauqua Hills as being *Quercus marilandica*, *Q. stellata*, and *Q. velutina*. Miller (1932), Caldwell (1937), other early survey records, and a few historical accounts include mention of the trees of this area. A few publications, Gates (1940), Cockrum (1952), and Fearing (1952) have included discussions and maps which involve the vegetation of this area to some degree. Other publications have been produced which give lists of species found in the various counties of the Chautauqua Hills area. Some of these are Gates (1940), Stevens and Dill (1940), Horr and McGregor (1949, 1951), McGregor (1950, 1956), Humfeld (1951), McGregor and Horr (1949, 1950, 1953, 1955), McGregor and Volle (1950), Yokoyama and McGregor (1951), McGregor and Hartman (1956), McGregor and Lathrop (1957), and Lathrop (1957). Previous to the present study, extensive field work had been done in the area by Dr. Ronald L. McGregor of the Department of Botany, University of Kansas. As a result, many plant specimens are on file at the University of Kansas Herbarium which supplemented the writer's collections. Dr. W. H. Horr and Mr. B. L. Wagenknecht have also collected numerous specimens from this area.

Up to this time, no one has made a study of the vascular flora of the Chautauqua Hills area of Kansas. Since it is in a region of transition of other vegetation areas, it was felt that a floristic and ecological study of the Chautauqua Hills would be a worthwhile addition to the knowledge of Kansas plants.

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CLIMATE

Annual temperatures (° F.) for the Chautauqua Hills computed from records covering the years 1898-1942.

Mean maximum	*Normal*	*Mean minimum*
68.6	58.4	46.7

Annual precipitation (inches) for the Chautauqua Hills computed from records covering the years 1898-1942.

Maximum, yr. 1915	*Normal*	*Minimum, yr. 1936*
52.68	37.70	29.52

Average dates of the killing frost and the average growing season for the Chautauqua Hills based on all available records through 1945.

Average date of the first killing frost in fall—October 23.

Average date of the last killing frost in spring—April 14.

Average length of the growing season—192 days.

ORIGINAL VEGETATION

A knowledge of the vegetation of the Chautauqua Hills before the time of settlement between the years 1870 and 1880 must be gained largely from surveyors' notes and writings of early residents of the area. These written records include mention of native plants from time to time. However, such mention was usually casual, and the exact species frequently could not be determined. Supplemental information was derived from oral statements of long time residents of the area concerning the early vegetation and from data of tree ring counts. The latter information was obtained by removing small cores of wood from 83 upland trees in the area by means of an increment borer. From these cores it was possible to estimate the approximate age of the tree by counting the annual growth rings. The counts indicate that many upland trees now

growing in the area were already there in the early and middle eighteen hundreds before the area was settled by the white man. Six *Quercus stellata,* ranging in diameter from 12 to 20 inches, dated from the year 1852 to as far back as 1769. One *Q. marilandica,* 17.6 inches in diameter dated back to 1851. For 11 trees, 5 *Q. stellata,* 5 *Q. marilandica,* and 1 *Q. velutina,* ranging in diameter from 10 to 19 inches, growth rings showed that they began their growth during the 1870's.

Additional evidence that the Chautauqua Hills were wooded before and at the time of settlement is to be found in the original surveyors' notes of the area. These records are on file at the State Auditor's Office in the State House and at the Kansas State Historical Society, Topeka, Kansas. These notes, taken in the field during the surveys of township and section lines between the years 1856 and 1877, include mention of the kinds, and in some cases, the diameter of trees on or near the lines. A general description of the land in the area of the surveys was sometimes recorded by the surveyors.

Frequent mention is made, in these notes, of blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and to a lesser extent, black oak (*Q. velutina*) as occurring in the uplands of the Chautauqua Hills. The diameters listed for these species were, on an average, slightly larger than for the same species today, being from 6 to 20 inches. However, several diameters of from 24 to 30 inches were recorded for the above species, indicating that at least some of the trees, growing at the time of settlement, were of even older age than those of the present.

Descriptions of the area of the Chautauqua Hills while it was still in undisturbed condition, were included in these Public Land Survey notes. The surveyors described the vegetation and physiography with respect to specific landmarks that can be easily located at the present time. Their descriptions of the areas surveyed are quoted below, in part.

(The present site of Yates Center, Wodson County, 1856.) "Timber black jack open woods, land graveley prairie. Land south part of black jack ridge, third rate — north part level first rate timber of black jack, post oak, hickory (*Carya*), and black walnut (*Juglans nigra*)."

(Two miles west of Yates Center, 1856.) "Land very broken with large sandstone on surface. Timber oak (*Quercus*), hickory, black walnut, black jack, and bur oak (*Quercus macrocarpa*), un-

dergrowth the same." (Chautauqua Hills area between Verdigris and Fall rivers, 1866.) "On either side of the two to three mile wide valley of the river (Verdigris) are broken ridges, the outcrops of rock being chiefly sandstone. Bluff soil poor, valley of Verdigris and smaller valleys have a rich alluvial soil covered with a fine vegetable mold. There is a belt of superior timber along the river and the hills are in several places covered with a young growth of post and black oak . . . Timber is abundant in the valleys and in many places is found in considerable quantities upon the bluffs . . . Almost entire surface is rolling and broken . . . with sandstone outcrops . . . The naturally rich, well timbered, and beautiful valleys of Indian Creek and Fall River . . . timber along Fall River composed of red elm (*Ulmus rubra*), white elm (*U. americana*), bur oak, hackberry (*Celtis*), oak, black walnut, sycamore (*Platanus occidentalis*), soft maple (*Acer saccharinum*), cottonwood (*Populus deltoides*), mulberry (*Morus*), coffee bean (*Gymnocladus dioica*), and buckeye (*Aesculus*). Undergrowth the same plus willow (*Salix*) and paw paw (*Asimina triloba*) . . . Along the bluffs and on the ridges there are large bodies of inferior scrub oak (*Quercus stellata* and *Q. marilandica*) . . . elsewhere a broken prairie except along the Verdigris and Fall Rivers."

In the year 1857 a surveying party, led by Col. Joseph E. Johnston, surveyed the southern boundary of the Kansas Territory. The party crossed the Chautauqua Hills along the southern line of present Chautauqua and Montgomery counties. Descriptions of the area, taken from the private journal of Col. Johnston and recorded by Miller (1932), are quoted below, in part.

(Approaching the Chautauqua Hills area from the east.) "The line today ran parallel to Russell Creek . . . the country gently undulating and soil rich black loam, limestone showing itself occasionally. Woodlands two or three miles to the southeast on the crest of a ridge beyond the creek." (On the divide between 12 Mile Creek and an affluent of the Verdigris.) ". . . the latter runs to the southwest in a broad and beautiful valley, the western side of which is abrupt, wood scattered through it." (Northeast part of present Coffeyville, Montgomery County.) "An Osage village of 27 huts, a half mile west of the ford (of the Verdigris River), the inhabitants buffalo hunting. . . . Two miles to the south is Nickeokaka (Onion Creek), well wooded. . . . Went to the crest of the ridge this side of the Little Verdigris (North

Caney Creek; Map 2) from which . . . the country appeared to be much more broken and wooded than the east side of the Verdigris . . . in 5 miles reached the Little Verdigris . . . moved on to a little south of west to avoid rugged hills. . . . The country, especially to the north, very broken. A good deal of oak in the heights . . . passed over a rugged ridge covered with post oak." (Approximately 2 miles west of Hewins, Chautauqua County.) "Our last camp (near Elgin, Chautauqua County) was just with timbered country. The march today was in prairie. The dividing ridge opposite is a plateau (Flint Hills) about 300 feet above this valley; the sides very abrupt and rocky. Limestone near the summit."

Similar notes were taken by Hugh Campbell, astronomer on the same survey. His descriptions of the area are recorded by Caldwell (1937) and are quoted below, in part. (Approximately 3 miles southeast of the present Coffeyville, Montgomery County.) "After crossing Pumpkin Creek we found ourselves ascending beautiful heights or uplands covered with the most luxuriant grass and other vegetation, particularly flowers of various colors . . . As the ascent continues, little specks of timber can be seen in all directions . . . on some of these (small streams) I found great numbers of wild rose bushes." (Along the march westward.) "The country over which we pursued our course presented a different aspect to that hitherto traversed. Ridges, mounds, and small elevated tablelands, covered with a luxuriant growth of vegetation, intersected with lines of timber marking the courses of gullies or small streams, now occupies the view. The country as far as the eye can see has the same broken and irregular appearance . . . Encamped on a small stream, the banks of which are well wooded with sycamore, cottonwood, and hackberry." (At Horse Head Creek.) ". . . well timbered on the west bank with oak, cottonwood, sycamore, walnut and cherry (*Prunus.*) The country on this day's march is still more abrupt and broken . . . passed over many ridges very rocky and covered with dense growth of black jack." (At present Caney City, Montgomery County.) "Passed through a large grove of post oak."

(Slightly west of Elgin, Chautauqua County.) ". . . the grass here, as well as on the neighboring highlands is excellent. The principal productions are as follows: Vis. Timber in immediate vicinity of river consists of oak sycamore, and walnut . . . Fish: Cat, trout or bass, buffalo and garr. Game: Deer, antelope, and turkeys are very numerous."

Public Land Surveys were not carried out in the southern part of the Chautauqua Hills until approximately 14 years after the northern half was surveyed. Descriptions of the area in survey notes of 1871 are quoted below, in part.

(Approximately 6 miles northeast of Sedan, Chautauqua County.) "Timber along stream (Middle Caney Creek) of elm, sycamore, walnut, ash (*Fraxinus*), and hackberry. Undergrowth of vines . . . Water (of the stream) clear and pure . . . Timber on upland post oak."

(The vicinity of present Elk Falls, Elk county.) "Creek bottoms . . . are well watered by many fine springs from the bluffs. Clear Creek, Wild Cat Creek, and Elk River are well timbered . . . ash, walnut, oak, hackberry, and sycamore. There are also several groves of upland timber consisting of black jack and post oak. . . ."

(General description of the land eight miles north of Sedan, Chautauqua County.) ". . . mostly high broken prairie covered with sandstone . . . eastern portion covered with black jack and post oak." (T30S, R12E, east central part of Elk County.) "Center of township is rough, rolling, and broken by ravines . . . the hills covered with a scrubby timber known as post oak and blackjack . . . Prairie covered with sandstone."

(T33S, R14E, west central part of Montgomery County.) "Land mostly second rate . . . except in the eastern and western portion of the township where there are high mounds rising from the rolling prairie, composed of sandstone. Timber on mounds post oak and black jack. Along streams elm, sycamore, and cottonwood."

The notes of the early surveyors for this area seemed to be consistent in mentioning timber for both uplands and bottomland. Upon examination of the notes, however, there are indications that the upland timber was not as dense as it is today. In listing trees which were marked at section and township corners, their distance from the corner is given and often their space relationship to other trees. Frequently these distances were relatively far and many times mention is made that no other trees were near or available to mark.

The uplands were not one continuous woods. The notes include mention of considerable upland hilly prairie over sandstone which was not wooded, just as it is today. Also the relatively large diame-

ters given for many of the upland trees indicate that they would have likely been well spaced.

Statements from Lockhart (1927), concerning the history of Elk Falls, Elk county, include, "The first settlers arrived over two trails, one from Independence country following the river (Elk) valley, which was covered with bluestem grass higher than the back of an ox. . . . Historical incidents and facts recollected by some of the older residents of the vicinity: Mr. Wert Wicker remembers when places, now covered with a dense growth of timber, could have been mowed, and some, at that time, (1877-79) actually were hay fields; Mr. George Bennett remembers when the bluestem grass was dense everywhere on the prairie and no country roads were marked, and few fields were broken."

General descriptions of the counties in the area of this study written by Andreas (1883) are quoted below, in part.

(Woodson County.) "The county is largely upland . . . Along the streams are belts of timber . . . averaging a half mile in width. In these belts are found oak, elm, hickory, black walnut, hackberry, sycamore, and cottonwood. (Greenwood County.) "It is . . . 5 percent of forest and 95 percent of prairie." (Elk County.) "The surface of the county is chiefly high, broken prairie, particularly back from streams, and in the western part the prairies are of increased elevation, rising into what are known as the Flint Ridges (Flint Hills). The uplands . . . although rocky and light of soil, produce abundant grasses . . . being supplied with abundance of clear running water." (Wilson County.) "Along the streams are timber belts . . . embracing oak, hickory, walnut, hackberry, elm, soft maple, pecan (*Carya illinoensis*), sycamore, ash, cherry, basswood (*Tilia*), and some cedar (*Juniperus virginiana*)." (Chautauqua County.) "The county is covered with a rich growth of wild grasses . . . and an abundant growth of timber . . . in some places it covers the hills and draws . . . the timber . . . upon the bluffy lands is made up of a species of oak vulgarly known as 'black jack.'" (Montgomery County.) "Timber, as in most parts of the state, is scarce, being confined to the belts along the water courses . . . occasional groves are found upon the uplands, but the timber is limited, and of inferior quality."

Early township maps of the area often showed the extent of forests. These maps were made up solely on the basis of data

written in the early surveyors' notes previously mentioned. These maps show that most of the uplands in the Chautauqua Hills, which are wooded at present, were covered by forests, to a slightly less extent, at the time of the surveys (1856 and 1871).

Further information concerning the distribution and spread of the forests is afforded by interviews with elderly residents who have lived in the Chautauqua Hills for all or most of their lives. Their recollections of the extent of timber on the uplands is as follows: C. C. Cox of Elk City, Montgomery County, stated that the scrub oak has increased a lot as far back as he can remember (to the 1890's). What used to be just a few blackjack near his farm is now a forest of the same. He recalled a prairie area that is now a scrub oak woods. He said that some hills were bare when he was young, but that there were scattered trees on most of the hills of the area; Art Oliver of Elk City can recall trees being on the hills and prairie hills as far back as 1897. He said that the oaks scattered into the prairie before hedge rows were planted and that they have spread down over the hills. He said that there is more post oak and blackjack now than 60 years ago, but that there has always been some on these hills. Mr. Oliver said that his father once pointed out a hill to him and stated that when the mature trees there were cut down, the forest that came afterwards was more dense; William Row of Toronto, Woodson county, remembered his father telling him that there was scattered post oak on the hills at the time of settlement. Mr. Row said that there has been an increase of the post and blackjack oak in the area in the last 65 years; Joe Dexter of Longton, Elk county, said that the woods on the hills of the area looked about as they do now as far back as he could remember; Frank Burtenshaw of Elk City, Montgomery county, stated that the scrub oak on the hills covers more area now than it did 50 to 60 years ago and that the trees have spread from the hilltops onto the slopes and into ravines. He stated that the mature trees had been cut in the past and that the growth that replaced it was thicker; Johnny Wilson of Havana, Montgomery county, said that the trees have increased on the hills and have spread. He remembered areas which used to be maintained as hay fields that are now forested. He stated that mowing and burning of hay fields and open woods kept down saplings of scrub oak and that the latter grew up as dense timber after mowing and burning ceased, allowing the young growth to continue year after year.

Following a study of the list of native trees of the Chautauqua

Hills as compiled from historical records, one is impressed by the fact that it corresponds with the common trees of the present woodlands of the area. It is significant that there is frequent mention of trees on the uplands of the area under consideration because Kansas has usually been thought of as being barren of trees except along water courses and valleys.

A statement by Fitch and McGregor (1956), concerning a woodland study in northeastern Kansas, applies equally well to this area. "The belief that this and similar areas in northeastern Kansas were virtually treeless at the time of occupation by white settlers is shown to be wholly unfounded by the information obtained from growth rings." For the Chautauqua Hills area, information from survey notes and other historical accounts can be added to the latter evidence.

PRESENT VEGETATION

With the disturbance by the plow, ax, and grazing, the changes in the vegetation of the Chautauqua Hills since settlement has been considerable. These changes have been not so much changes in composition as in extent of area covered. Evidence indicates that there is more forest and much less prairie now than before settlement. It is probable that regular burning of prairies kept back the spread of scrub oak as did mowing and burning in prairie woodlands by the settlers. Much of the upland timber was cut down 60 to 70 years ago by the early settlers for fuel and lumber. Since that time the trees have reproduced from seed, and much second growth has developed from the stumps and suckers from roots. Since fire has been under control, trees have advanced down slopes and into prairie uplands as far as the environment permitted.

Most of the lowland and some of the upland prairie was plowed for cultivation. Much of the latter area is in use now for grazing and native hay but is by no means in an undisturbed condition. Yates Center, in Woodson county, is considered the prairie hay capital of the world. Of the 2,678,440 acres in the Chautauqua Hills area, 188,511 acres were in native hay in 1936 and 107,370 acres in 1952.

Disturbance has allowed for invasion of plants into fields and overgrazed pastures. Besides invasion of weeds into these places, some trees have become established also.

There is great diversity of plant groupings in the Chautauqua Hills ranging from marsh to flood plain woods, prairie, and rocky

wooded gullies. The following habitats are typical and representative of the plant communities in the Chautauqua Hills area.

Upland woods: These forests exist in continuous to scattered stands (Map 1) on sandstone of the Douglas group (Map 2) throughout the Chautauqua Hills. The forests are characteristically located over low rolling uplands (Plates 1, 3, and 5; Fig. 2) and cap prairie hilltops in numerous places (Plate 2). However, the aspect of the upland woods changes from place to place. Where these woods border gullies, ravines, and flood plains, the slopes are usually wooded their entire extent (Plates 4 and 5). In prairie areas the upland woods are generally restricted to the upper slopes and high places (Plates 1 and 2). In such areas, *Quercus stellata* and *Q. marilandica* among others (Tables 1 and 4), grow on rough, rocky land where run in water is received from sandstone surfaces and where snow lodges during the winter. These trees are located well above the water table and must withstand varying periods of drought. Seedlings do not become established on lower prairie slopes because the grasses are better equipped to obtain the available moisture.

To understand better the composition of the upland woods, the trees in 16 representative areas throughout the Chautauqua Hills were sampled by 45 strip transects. With these, the species and diameter of the first 100 trees occurring in a strip two meters wide were recorded. The data of transects which were taken in areas showing a similar aspect were tabulated and the percentages of the trees by size class were worked out (Tables 1-5).

The distribution of other *Quercus stellata—Q. marilandica* type woodlands are included in the writings of several workers. The oak-hickory forest region, as recognized by Braun (1950) extends from Canada to Texas as the westernmost part of the Eastern Deciduous Forest. A *Q. stellata—Q. marilandica* type woods, among others, is listed as occurring in the Piedmont (oak-hickory region of North Carolina) by Bourdeau (1954). His statements are quoted below, in part.

"The post oak—black jack oak forest (or the Piedmont) is called preclimax or subclimax by Oosting (1942). From a polyclimax point of view . . . it would be a physiographic or edaphic climax . . . Whatever the terminology used, post oak—black jack oak forests are restricted, in the North Carolina Piedmont, to dry south facing bluffs, thin rocky soils, strongly eroded soils, or to

the Iredell, Orange, and other closely related soil series . . . Trees in these sites are slow growing, rarely exceeding 30 feet in height . . . the stands are poorly stocked and do not form a closed canopy."

Braun (1950) lists similar communities of *Quercus stellata—Q. marilandica*, which exist throughout the Oak-Hickory Forest region, as follows: (1) in the Flatwoods Belt of Alabama and Mississippi, a flat area of heavy soils, water logged during rainy periods, dry and hard at other times; (2) on the poorest soils in the uplands of the Coast Plain west of the Mississippi River; (3) on drier ridges with sandy slopes and on steep more or less southerly slopes of the Ozark Plateau, the Boston Mountains, and the Ouachita Mountains; (4) on the open xeric plateau of the western border of the Ozarks; (5) on extensive areas of the old Kansas drift (Mississippi Valley); (6) on the Illinoian drift area (Prairie Peninsula section). The *Quercus stellata—Q. marilandica* communities are also represented in the Oak-Chestnut, the Western Mesophytic, and the Mixed Mesophytic forest regions.

In discussing the Oak-Hickory Association, Oosting (1956) stated that throughout the association, various combinations of oak and hickory may occur as preclimax. His illustration was the *Quercus stellata—Q. marilandica* which occurs widely on poor sites and dry exposures in the association. In Texas and Oklahoma the above species occur in open, savannalike stands, known as Cross Timbers (Dyksterhuis) 1948, which mark the transition to grassland in that area.

Rice and Penfound (1956) list *Quercus stellata* and *Q. marilandica* as dominants in the deciduous forest frontier in Oklahoma extending in a strip about 140 miles wide east of U. S. 81 and extending from Kansas to Texas.

The upland woods of the Chautauqua Hills extend through Oklahoma and on south to the Cross Timbers in Texas.

Several communities of *Quercus stellata—Q. marilandica* also occur as isolated stands on low sandstone capped hills in outlying areas of the Chautauqua Hills and in limited areas of the extreme southeastern corner of Cherokee County, Kansas. Fitch and McGregor (1956) reported a few small groves on slopes of a woodland area in Douglas County, Kansas. McGregor (1948) listed *Quercus marilandica* as being dominant in some strictly sandy soils of hillsides in the latter county.

In the understory of the upland woods (Plate 3; Fig. 2), shrubs such as *Symphoricarpos orbiculatus, Rhus copallina, R. glabra, Rubus allegheniensis, R. flagellaris,* and *R. occidentalis* grow beneath the trees and along margins of the woods. Numerous other characteristic species are found and can be listed as spring, summer, and fall aspects. Species in the spring aspect are usually evident because of their coloration. Several species of the woodlands come out early in the spring, have a short growth and die down. Characteristic of such are *Hedyotis minima, Androsace occidentalis, Claytonia virginica, Viola pedata, V. papilionacea, Draba reptans, D. brachycarpa,* and *Sibara virginica.* Some of the other common species of the spring aspect in upland woods are *Erythronium mesochoreum, Chaetopappa asteroides, Viola kitaibeliana* var. *rafinesquii, Erysimum repandum, Corydalis crytallina, Arenaria patula, Geranium carolinianum, Antennaria fallax, Nothoscordium bivalve, Galium aparine, Hypoxis hirsuta,* and *Fragaria virginiana.*

Species of sedges which are common at this time are *Carex blanda, C. pensylvanica, C. bicknellii, Eleocharis obtusa,* and *E. engelmanni.* Some of the rushes, which appear shortly after the sedges, are *Juncus torreyi, J. marginatus* var. *setosa,* and *J. interior.*

For a period of a few weeks after the peak of the spring aspect is past, few new species appear, after this the summer aspect becomes evident. It is not as colorful as the spring aspect, but many species are conspicuous for their relative large size. Characteristic of the latter are *Tephrosia virginica, Amorpha canescens, A. fruticosa, Desmodium illinoense, D. sessilifolum, D. glutinosum, Cassia fasciculata, Lespedeza virginica, Apocynum cannabinum, Hieracium gronovii, Liatris squarrosa, Aster patens, A. ericoides, Chrysopsis pilosa,* and *Solidago ulmifolia.*

Other less conspicuous species making up the understory of the summer are *Plantago virginica, P. purshii, P. aristata, Polytaenia nuttallii, Talinum parviflorum, Polygala incarnata, P. sanguinea, Lechea tenuifolia, Cyperus filiculmis, C. ovularis,* and *Parietaria floridana.* Some of the more common grasses of the summer aspect are *Boutelous hirsuta, Muhlenbergia racemosa, M. brachyphylla, Paspalum ciliatifolium,* and *Festuca ovina.*

In the fall the understory of the upland woods is made up of numerous species of grasses as well as several colorful flowering species. A few of the grasses are *Andropogon scoparius, Sporobolus asper, Aristida dichotoma, A. purpurascens, Muhlenbergia*

capillaris, Panicum agrostoides, P. spaerocarpon, Leersia oryzoides, and *Agrostis hiemalis.* Other species of plants characteristic of the fall aspect are *Liatris scariosa, Desmodium marilandicum, Spiranthes cernua, Acalypha gracilens, Solidago missouriensis* var. *glaberrina, Conyza canadensis,* and *Oxalis europaea.*

Prairie: The prairie which once covered much of the Chautauqua Hills is now confined to a few hay fields, considerable pasture, and to a few relics along railroad right of ways, and roadsides (Plates 1, 6, and 20: Fig. 2).

TABLE 1. Percentages of Tree Species by Size Class on Hilltops and Slopes of Rolling Upland Woods

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Hilltops:							
Celtis occidentalis	.25						.25
Cornus drummondi	.25						.25
Juniperus virginiana	.12						.12
Morus rubra	.12	.12					.24
Quercus marilandica	18.0	4.0	2.5	1.6			26.1
Quercus prinoides	.8	.5					1.6
Quercus stellata	48.5	12.7	6.1	2.25	.25		69.8
Quercus velutina	.12						.12
Ulmus americana	.12						.12
Ulmus rubra	1.7						1.7
North slopes:							
Carya cordiformis	2.1	.5					2.6
Carya ovata	.3						.3
Celtis occidentalis	.6						.6
Cercis canadensis	.3						.3
Cornus drummondi	.1						.1
Crataegus sp.	.1						.1
Fraxinus americana	.1						.1
Juglans nigra	.6						.6
Juniperus virginiana	.1						.1
× *Quercus fernowi*	1.3						1.3
Quercus marilandica	12.1	4.0	4.5	1.0	1.0		24.3
Quercus prinoides	2.1						2.1
Quercus stellata	38.3	11.0	7.3	2.1	.6	.16	57.8

Table 1. Percentages of Tree Species by Size Class on Hilltops and Slopes of Rolling Upland Woods—*Concluded*

Species	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
North slopes—*Concluded*							
Quercus velutina	3.6	1.3	3.0	.5	.....	.1	8.5
Ulmus americana	.1	.1	.....	.....	.....	.....	.2
Ulmus rubra	1.0	.....	.....	.....	.....	.....	1.0
South slopes:							
Juniperus virginiana	1.5	.....	.....	.....	.....	.....	1.5
Quercus marilandica	9.5	7.5	6.0	1.0	.....	.....	24.0
Quercus stellata	28.5	25.0	15.5	4.0	1.5	.....	74.5

TABLE 2. Percentages of Tree Species by Size Class in Gullies and Slopes of Upland Woods

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Crests of gullies:							
Quercus marilandica	19.0	18.0	10.0	4.5	2.0	4.5	58.0
Quercus stellata	30.0	9.0	2.0	1.0	.....	.....	42.0
North slopes:							
Juniperus virginiana	2.0	.....	.....	.....	.....	.....	2.0
Quercus marilandica	32.0	10.0	8.0	1.0	2.0	1.0	54.0
Quercus stellata	30.0	15.0	10.0	4.0	1.0	.....	60.0
Ulmus americana	1.0	.....	.....	.....	.....	.....	1.0
South slopes:							
Quercus marilandica	6.0	7.0	1.0	.....	1.0	.....	15.0
Quercus stellata	49.0	22.0	10.0	.....	3.0	.....	84.0
Ulmus rubra	1.0	.....	.....	.....	.....	.....	1.0
East slope:							
Carya cordiformis	2.0	.....	.....	.....	.....	.....	2.0
Cercis canadensis	2.0	.....	.....	.....	.....	.....	2.0
Morus rubra	1.0	.....	.....	.....	.....	.....	1.0
Prunus serotina	1.0	.....	.....	.....	.....	.....	1.0
Quercus marilandica	20.0	16.0	21.0	15.0	5.0	6.0	83.0
Quercus stellata	8.0	2.0	.....	.....	1.0	.....	11.0

TABLE 2. Percentages of Tree Species by Size Class in Gullies and Slopes of Upland Woods—*Concluded*

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Gullies:							
Carya cordiformis	10.0	.5					1.0
Carya ovata	1.5						1.5
Celtis occidentalis	1.0						1.0
Cercis canadensis	14.0						14.0
Cornus drummondi	3.5	1.0					4.5
Cornus obliqua	1.0						1.0
Crataegus mollis	3.0						3.0
Euonymus atropurpureus	.5						.5
Juglans nigra	2.5	.5	.5				3.5
Juniperus virginiana	1.0						1.0
Platanus occidentalis	4.0		1.0	.5	1.0		6.5
Populus deltoidcs	1.5						1.5
Prunus serotina	.5						.5
Quercus macrocarpa	4.0	2.0	5.5	4.5	.5		16.5
Quercus marilandica	3.5	1.0	1.0				5.5
Quercus muehlenbergii	5.5	.5		.5			6.5
Quercus shumardii var. *scheckii*	.5	.5					1.0
Quercus stellata	4.0	1.0	.5				5.5
Quercus velutina	1.0	1.0				.5	2.5
Salix nigra	1.0						1.0
Salix caroliniana	.5						.5
Ulmus americana	.5						.5
Ulmus rubra	4.5	.5	.5				5.5
Viburnum rufidulum	8.0	.5	.5				9.0

TABLE 3. Percentages of Tree Species by Size Class in Flood Plains and Bordering Uplands

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Crests of bluffs:							
Juniperus virginiana	.5						.5
Quercus marilandica	20.5	11.0	5.5	1.5	1.0		42.0
Quercus stellata	34.0	13.0	8.5	.5	.5		57.0
Quercus velutina		.5					.5
North slopes:							
Carya cordiformis	5.5	.5					6.0
Carya ovata	5.5						5.5
Celtis occidentalis		.5					.5
Celtis tenuifolia var. *georgina*	.5						.5
Cercis canadensis	4.0						4.0
Fraxnius pennsylvanica var. *subintegerrima*	1.5						1.5
Juglans nigra				.5	.5		1.0
Juniperus virginiana	1.0						1.0
Maclura pomifera	1.0						1.0
Platanus occidentalis	1.5		.5			.5	2.5
Quercus macrocarpa	4.0						4.0
Quercus marilandica	20.5	4.0	2.0	.5	1.0		28.0
Quercus stellata	10.5						10.5
Quercus velutina	9.5	1.0	.5	.5		1.0	12.5
Staphylea trifolia	2.5						2.5
Ulmus americana	4.5	1.0	2.5	.5	.2		9.5
Ulmus rubra	2.5	.5	1.0				4.0
Viburnum rufidulum	5.5						5.5

Table 3. Percentages of Tree Species by Size Class in Flood Plains and Bordering Uplands—*Concluded*

Species	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
South slopes:							
Quercus marilandica	47.0	12.0	4.0	2.0	.....	.....	65.0
Quercus stellata	25.0	5.0	.....	.....	.....	.....	35.0
Flood plains:							
Acer saccharinum	.....	.....	.5	.5	1.5	2.0	4.5
Asimina triloba	6.0	.....	.....	.....	.....	.....	6.0
Carya cordiformis	3.0	4.0	2.5	.5	.....	.....	10.0
Carya ovata	4.0	.....	.....	.....	.....	.....	4.0
Celtis occidentalis	4.5	1.5	.....	1.0	.5	2.0	9.5
Cercis canadensis	1.5	.....	.....	.....	.....	.....	1.5
Euonymus atropurpureus	1.0	.....	.....	.....	.....	.....	1.0
Fraxinus pennsylvanica var. *subintegerrima*	3.5	.....	.....	1.5	.5	.....	4.5
Gymnocladus dioica	.5	.5	.5	.....	.....	1.0	2.5
Juglans nigra	1.5	.....	.5	.5	.5	.....	3.5
Maclura pomifera	1.0	.....	.....	.....	.....	.....	1.0
Morus rubra	4.5	1.5	.....	.....	.....	.....	6.0
Platanus occidentalis	.....	1.0	.....	.....	.....	.....	1.0
Quercus macrocarpa	7.5	4.5	2.5	.....	.....	.....	14.5
Quercus marilandica	.5	.5	.....	.....	.....	.....	1.0
Quercus stellata	1.0	.....	1.0	.....	.....	.....	2.0
Quercus velutina	5.5	1.5	2.5	3.5	.....	.....	12.0
Staphylea trifolia	1.0	.....	.....	.....	.....	.....	1.0
Ulmus americana	6.5	3.0	1.0	1.0	.....	.....	11.5
Ulmus rubra	2.5	.5	.....	.....	.....	.....	3.0

TABLE 4. Percentages of Tree Species by Size Class in Upland Woods Surrounded by Prairie

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Hilltops:							
Carya cordiformis	.6						.6
Juniperus virginiana	.3						.3
Prunus serotina	.3						.3
Quercus marilandica	36.0	19.3	8.0	5.0	2.3	.4	67.3
Quercus prinoides	2.3						2.3
Quercus stellata	22.0	4.0	.6	.6	.6		28.3
Ulmus rubra	.3						.3
Viburnum rufidulum	.6						.6
North slopes:							
Carya cordiformis	1.6						1.6
Juglans nigra	.3						.3
Morus rubra	.3						.3
Prunus serotina	.3						.3
Quercus marilandica	54.0	6.0	4.6	.6	.3	.6	66.3
Quercus prinoides	1.0						1.0
Quercus stellata	22.6	4.0		.6			28.3
Ulmus americana	.6						.6
Viburnum rufidulum	1.3						1.3
South slopes:							
Juglans nigra	.5						.5
Quercus marilandica	30.5	17.5	4.5	2.0	.5		54.0
Quercus stellata	33.5	10.0	2.0	.5			45.5

Table 5. Percentages of Tree Species by Size Class in Ravines and Slopes of Upland Woods

Species	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Crests of ravines:							
Fraxinus pennsylvanica var. *subintegerrima*	1.5						1.5
Juniperus virginiana	.5						.5
Quercus marilandica	14.0	6.5	6.0	1.5	.5		28.0
Quercus stellata	50.0	12.5	4.5	1.5		1.5	70.0
North slopes:							
Celtis occidentalis	1.0						1.0
Fraxinus pennsylvanica var. *subintegerrima*	3.0						3.0
Juniperus virginiana	2.0						2.0
Quercus marilandica	20.0	8.0	1.0				29.0
Quercus stellata	50.0	8.0			2.0	3.0	63.0
South slopes:							
Fraxinus pennsylvanica var. *subintegerrima*			1.0				1.0
Juniperus virginiana	3.0						3.0
Quercus marilandica	20.0						20.0
Quercus stellata	50.0	20.0	2.0	2.0	2.0		76.0
West slopes:							
Carya cordiformis	2.0						2.0
Carya ovata	3.0	5.0					10.0
Cercis canadensis	1.0						1.0
Maclura pomifera	1.0						1.0
Quercus marilandica	14.0	4.0	1.0	1.0			20.0
Quercus muehlenbergii	2.0	1.0	1.0				4.0
Quercus stellata	34.0	8.4	5.0	3.0			50.0
Quercus velutina	6.0		2.0			1.0	9.0
Viburnum rufidulum	2.0		1.0				3.0

TABLE 5. Percentages of Tree Species by Size Class in Ravines and Slopes of Upland Woods—*Concluded*

SPECIES	Size class in inches based on diameter at breast height						
	0–5	6–7	8–9	10–11	12–13	14–	Total %
Ravines:							
Aesculus glabra	4.0						4.0
Carya cordiformis	3.0	1.5	3.0	1.0			8.5
Carya ovata		.5			.5	.5	1.5
Celtis tenuifolia var. *georgiana*	1.0						1.0
Cercis canadensis	13.0						13.0
Cornus drummondi	1.5						1.5
Cornus obliqua	4.0						4.0
Crataegus mollis	1.0						3.0
Fraxinus americana	3.5	.5	1.0	.5			5.5
Fraxinus pennsylvanica var. *subintegerrima*	3.0		.5				3.5
Gleditsia triacanthos	1.0						1.0
Juglans nigra	2.0	.5	1.0	1.0	1.5		6.0
Juniperus virginiana	3.5	.5				.5	4.5
Maclura pomifera	3.0						3.0
Morus rubra	.5						.5
Platanus occidentalis	3.5			.5			4.0
Populus deltoides	.5						.5
Quercus macrocarpa	1.0		1.5		1.5	1.0	4.0
Quercus muehlenbergii	2.5			.5	.5		3.5
Quercus prinoides	.5						.5
Quercus velutina	9.0	1.5	.5	1.0	.5	1.0	13.5
Salix nigra	.5						.5
Ulmus americana	.5						.5
Ulmus rubra	4.5	1.5	2.0	.5		2.0	10.5
Viburnum rufidulum	3.0						3.0

Weaver and Hansen (1941) state that, "Native true prairie, even when lightly grazed will retain essentially its original composition over a long period of time." It is when disturbance occurs that stages of degeneration become noticeable. There is no true undisturbed prairie in the area of this study. The major disturbance of the prairie of this region is overgrazing. Cattle, and to some extent, horses are the grazing animals involved. When grazing, and the resulting trampling, become excessive, the original cover can not be maintained (Plate 7). When forage is plentiful, there is selection and preference for certain types and species by livestock. Due to this, the remaining vegetation grows better. Continued grazing of this nature, especially early and close grazing, will cause these preferred species to disappear. Light, water, and minerals normally used by more palatable grasses, are now available to less desirable species. Thus, the latter may flourish and become established. The early change of composition in disturbed hay fields and pastures involves only a shift of the plant population normally components of the native prairie (Weaver, 1954). As the native grasses are weakened under grazing, bare places appear. This may happen because of the death of the plants, dunged areas, or where livestock has pawed or trampled. Invader species, better adapted to trampling and other grazing conditions, become established in these bare places (Plate 8). As the pasture continues to be disturbed, the original palatable grasses and forbs decrease, less palatable grasses and forbs increase, and as degeneration continues, all the original native grasses and forbs are replaced by undesirable invaders (Plate 9).

To understand better the degree of degeneration and composition of the prairie of the Chautauqua Hills, 27 prairie areas were sampled by line interception transects. The transect used was a 1,000 cm. line stretched and staked firmly in position in the area under consideration. The measurements included the intercept of each plant or clumps of the species encountered within 10 mm. on one side of the line. By dividing the total linear extent intercepted by each species, or all species, by the length of the transect and multiplying by 100, the percentage of ground cover (basal area) was ascertained. Dividing the length for each species by the total length of all species intercepted on the line and multiplying by 100 gave the percentage composition. Since the base of clumped species contains a certain number of dead individual plants, the actual percentage cover (basal area) is probably slightly less than that measured.

By using the transect data, field observations, and adapting the procedure of Weaver and Hansen (1941) and Hetzer and McGregor (1951), six more or less distinct stages of prairie degeneration were determined for the area of this study. The type of prairie is designated by the numbers 1 to 6 in decreasing order of deterioration as follows:

Prairie type No. 1 (Table 6). Ungrazed prairie with a uniform cover of *Andropogon scoparius* and *A. gerardi. Panicum virgatum* and *Sorghastrum nutans* are also characteristic, but to a lesser degree. Palatable legumes are the characteristic forbs, but are not abundant.

Prairie type No. 2 (Table 7). Grazed prairie in which the forage usually exceeds the needs of grazing animals. *Andropogon scoparius* is characteristically of high percentage composition. *A. gerardi,* when present on lower slopes, is of relative high percentage. *Bouteloua curtipendula,* due to the slightly degenerated condition of even good prairie areas, is commonly present, but of low percentage. *Panicum virgatum, P. dichotomiflorum,* and *Sorghastrum nutans* are also characteristic components of this prairie stage. Occasionally there is a noticeable amount of invader grasses such as *Eragrostis intermedia, Bromus secalinus,* and *B. japonicus.* The highest percentage of these grasses, however, occur in stands near gates, fences, or areas of irregular grazing. A few of the characteristic forbs when present are *Baptisia minor, B. leucophaea, Amorpha canescens,* and *Echinacea pallida.* Other forbs which may be present are, among others, *Euphorbia corollata, Verbena stricta, Solidago altissima, Salvia azurea* var. *grandiflora,* and *Ruellia humilis.*

Prairie type No. 3 (Table 8). Grazed prairie characterized by a decrease of *Andropogon scoparius* and an increase of *Bouteloua curtipendula* as compared to prairie type No. 2. The characteristic grasses in order of abundance are as follows. *Bouteloua curtipendula, Andropogon scorparius, Panicum virgatum, P. dichotomiflorum, Andropogon gerardi,* and *Sorghastrum nutans.* The cover is rather uniform except for occasional patches of *Bromus secalinus, B. japonicus, Eragrostis capillaris,* and *Chloris verticillata* in areas where invader grasses can get a hold. Forbs are not usually abundant, but the same species listed for prairie type No. 2 are present plus *Achillea lanulosa, Physostegia virginiana, Aster azureus, A. oblongifolius, Asclepias viridiflora, Psoralea tenuiflora, Erigeron strigosus, Liatris punctata,* and *Penstemon tubaeflorus.*

Prairie type No. 4 (Table 9). This stage of degeneration is characterized by a decrease of palatable legumes and by invader

species becoming established in open areas. The prairies show the effect of somewhat heavy grazing. *Andropogon scoparius* is almost completely absent. There is a decrease in *Bouteloua curtipendula* and an increase in grasses such as *Eragrostis capillaris* and *Chloris verticillata*. *Bromus japonicus* is found occasionally. Grasses not found in the previous stages, but present here are *Andropogon saccharoides, Eragrostis megastachya, Paspalum pubiflorum* var. *glabrum, Sporobolus asper,* and *Bouteloua hirsuta.* Characteristic forbs are *Baptisia minor, Dalea purpureum, Asclepias viridiflora, Solidago rugosa, Amorpha canescens, Achillea lanulosa* and *Ruellia humilis.* A number of weeds found in this type prairie are as follows: *Gaura coccinea, Kuhnia eupatorioides, Cirsium undulatum, Ambrosia psilostachys* var. *coronopifolia, Xanthocephalum dracunculoides,* and *Solanum rostratum.*

Prairie type No. 5 (Table 10). Characterized by being overgrazed in general. This type has a high percentage of invader grasses and weeds. *Andropogon scoparius* is completely gone and there is a marked decrease in forbs. *Bouteloua curtipendula* is still present but ranks in percentage along with *Aristida oligantha, Bromus japonicus, Paspalum ciliatifolium,* and *P. pubiflorum* var. *glabrum.* Additional weeds found in this stage are such species as *Croton monanthogynus, Plantago aristata, Vernonia baldwini* var. *interior,* and *Solanum americanum.*

Prairie type No. 6 (Table 11). The final stage of degeneration is characterized by the presence of numerous weeds, bare spaces, dense patches of *Chloris verticillata, Bromus japonicus, Eragrostis capillaris, E. intermedia, Buchloe dactyloides, Aristida oligantha,* and *Paspalum ciliatifolium,* and the absence of all original grasses. Occasional forbs such as *Achillea lanulosa, Ruellia humilis, Asclepias viridiflora, Dalea purpureum,* and *Teucrium canadense* may be present in small numbers. Species which are in by far greater abundance are, among others, *Solanum rostratum, S. americanum, Xanthocephalum dracunculoides, Plantago aristata, Cirsium undulatum, Croton monanthogynus,* and *Vernonia baldwini* var. *interior.*

The characteristic species of the prairie can be divided into spring, summer, and fall aspects. The spring aspect is colorful with blooming colonies of small plants and scattered individuals. The most common species of this kind are *Anemone caroliniana, Camassia scilloides, Baptisia minor, B. leucophaea, Phlox pilosa, Tradescantia ohiensis, Senecio plattensis, Verbena canadensis, Oxalis violacea, Astragalus caryocarpus, Ruellia humilis, Veronica arvensis, Oenothera triloba, Erigeron strigosus,* and *Callirhoe involucrata.*

TABLE 6. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 1.

AREA NO. 13. Ungrazed prairie 9 miles east of the Chautauqua Hills, Woodson County, NW ¼ Sec. 34, T25S, R17E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	20.0	2.23
Andropogon scoparius	67.0	7.15
Antennaria neglecta	1.23	.14
Aster azureus	2.8	.31
Bouteloua curtipendula	1.1	.12
Panicum virgatum	7.6	.82
Ruellia humilis	.27	.03
Total		10.8

AREA NO. 18. Ungrazed prairie 1 mile west of the Chautauqua Hills, Greenwood County, NW ¼ Sec. 34, T25S, R13E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	87.3	8.76
Bouteloua curtipendula	4.0	.41
Panicum virgatum	2.3	.27
Tridens flavus	6.4	.68
Total		10.12

AREA NO. 25. Ungrazed prairie in the Chautauqua Hills, Elk County, SW ¼ Sec. 33, T29S, R12E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	35.0	4.08
Andropogon scoparius	62.7	7.39
Eragrostis intermedia	1.0	.12
Sorghastrum nutans	1.3	.16
Total		11.75

TABLE 7. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 2.

AREA NO. 8. Grazed prairie in the Chautauqua Hills, Chautauqua County, NW ¼ Sec. 33, T33S, R12E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	78.7	7.8
Bouteloua curtipendula	4.5	.44
Bromus secalinus	10.3	1.0
Elymus canadensis	2.0	.23
Eragrostis capillaris	1.6	.16
Panicum dichotomiflorum	2.4	.23
Panicum sp.	.5	.05
Total		9.96
AREA NO. 9. Grazed prairie in the Chautauqua Hills, Chautauqua County, SW ¼ Sec. 33, T33S, R12E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	9.0	.80
Andropogon scoparius	57.0	5.03
Bouteloua curtipendula	18.0	1.48
Bromus secalinus	5.0	.44
Chloris verticillata	2.3	.21
Eragrostis capillaris	.3	.02
Panicum dichotomiflorum	4.0	.36
Panicum virgatum	2.3	.21
Plantago aristata	.7	.06
Sporobolus asper	1.4	.12
Total		8.70
AREA NO. 11. Grazed prairie 10 miles north of the Chautauqua Hills, Woodson County, NW ¼ Sec. 23, T23S, R15E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	68.0	6.54
Bouteloua curtipendula	.2	.13
Eragrostis intermedia	29.0	2.69
Panicum virgatum	2.4	.23
Solidago altissima	.4	.04
Total		9.63

TABLE 7. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 2.—*Concluded*

AREA NO. 19. Grazed prairie 1 mile east of the Chautauqua Hills, Wilson County, SE ¼ Sec. 15, T30S, R14E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	56.0	4.96
Bouteloua curtipendula	2.6	.21
Eragrostis intermedia	30.0	2.55
Panicum lanuginosum	.4	.02
Panicum virgatum	11.0	.97
Total	.....	8.71

TABLE 8. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 3.

AREA NO. 2. Grazed prairie 14 miles east of the Chautauqua Hills, Montgomery County, SW ¼ of NE ¼ Sec. 34, T34S, R17E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	36.0	3.16
Bouteloua curtipendula	51.4	4.50
Bromus secalinus	1.6	.14
Chloris verticillata	2.4	.21
Panicum dichotomiflorum	3.0	.26
Panicum virgatum	5.3	.47
Total	.....	8.76

AREA NO. 3. Grazed prairie 13 miles east of the Chautauqua Hills, Montgomery County, NW ¼ of SE ¼ Sec. 32, T34S, R17E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	42.2	5.1
Asclepias viridiflora	.4	.05
Bouteloua curtipendula	53.0	6.31
Echinacea pallida	1.0	.12
Eragrostis capillaris	.15	.02
Panicum virgatum	.6	.08
Psoralea tenuiflora	.25	.03
Sprorbolus sp.	2.4	.29
Total	.....	12.00

TABLE 8. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 3.—*Continued*

AREA No. 4. Grazed prairie 1 mile west of the Chautauqua Hills, Chautauqua County, SW ¼ Sec. 33, T32S, R11E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	37.5	3.74
Bouteloua curtipendula	46.7	4.65
Bromus secalinus	9.1	.89
Panicum dichotomiflorum	4.7	.45
Panicum virgatum	2.0	.18
Total		9.91
AREA No. 12. Grazed prairie 8 miles north of the Chautauqua Hills, Woodson County, NW ¼ Sec. 35, T23S, R15E.	Percent composition	Percent basal area
Species:		
Aster azureus	.23	.02
Bouteloua curtipendula	92.0	8.01
Liatris punctata	.51	.05
Panicum lanuginosum	.23	.02
Panicum virgatum	5.0	.41
Panicum sp.	1.60	.14
Ruellia humilis	.43	.04
Total		8.65
AREA No. 14. Grazed prairie 8 miles east of the Chautauqua Hills, Woodson County, SE ¼ Sec. 33, T25S, R17E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	2.4	.20
Andropogon scoparius	3.4	.29
Bouteloua curtipendula	81.0	6.97
Echinacea pallida	.5	.04
Elymus virginicus	2.5	.21
Panicum virgatum	6.0	.56
Panicum sp.	3.7	.32
Ruellia humilis	.5	.04
Total		8.34

TABLE 8. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 3.—*Concluded*

AREA No. 21. Grazed prairie 3 miles east of the Chautauqua Hills, Wilson County, NW ¼ Sec. 18, T30S, R15E.	Percent composition	Percent basal area
Species:		
Andropogon scoparius	4.3	.38
Bouteloua curtipendula	83.5	7.31
Bromus japonicus	10.5	.92
Opuntia macrorhiza	1.7	.15
Total		8.74

AREA No. 23. Grazed prairie in the Chautauqua Hills, Elk County, SE ¼ Sec. 9, T30S, R13E.	Percent composition	Percent basal area
Species:		
Amorpha canescens	.9	.08
Bouteloua curtipendula	75.3	6.74
Panicum virgatum	23.4	2.13
Ruellia humilis	.4	.03
Total		8.98

AREA No. 27. Grazed prairie 6 miles west of the Chautauqua Hills, Elk County, NW ¼ Sec. 2, T30S, R11E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	4.8	.41
Andropogon scoparius	16.0	1.46
Bouteloua curtipendula	61.7	5.23
Opuntia macrorhiza	1.5	.13
Panicum virgatum	14.0	1.23
Total		8.46

TABLE 9. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 4.

AREA No. 1. Grazed prairie 13 miles east of the Chautauqua Hills, Montgomery County, SE ¼ Sec. 33, T34S, R17E.	Percent composition	Percent basal area
Species:		
Andropogon saccharoides	42.4	4.00
Aristida oligantha	5.0	.46
Bouteloua curtipendula	13.0	1.20
Chloris verticillata	13.3	1.20
Croton monanthogynus	.2	.02
Eragrostis capillaris	2.6	.25
Eragrostis megastachya	3.1	.30
Erigeron strigosus	7.0	.60
Hieracium sp.	.6	.06
Paspalum sp.	.5	.05
Panicum virgatum	12.0	1.10
Rudbeckia serotina	.3	.03
Total		9.49

AREA No. 6. Grazed prairie 1 mile west of the Chautauqua Hills, Chautauqua County, SW ¼ Sec. 9, T34S, R11E.	Percent composition	Percent basal area
Species:		
Andropogon saccharoides	5.5	.37
Aristida oligantha	9.2	.63
Bouteloua curtipendula	42.0	2.71
Boutcloua hirsuta	30.0	1.93
Panicum dichotomiflorum	5.0	.32
Panicum lanuginosum	4.0	.26
Panicum virgatum	3.4	.22
Physostegia virginiana	.9	.06
Total		6.50

AREA No. 16. Grazed prairie 2 miles west of the Chautauqua Hills, Chautauqua County, NW ¼ Sec. 34, T25S, R13E.	Percent composition	Percent basal area
Species:		
Andropogon gerardi	1.7	.16
Andropogon scoparius	17.5	1.75
Bouteloua curtipendula	52.2	5.21
Bromus japonicus	14.2	1.41
Panicum virgatum	13.5	1.35
Salvia azurea v. *grandiflora*	.9	.09
Total		9.96

TABLE 9. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 4—*Concluded*

AREA NO. 22. Grazed prairie in the Chautauqua Hills, Wilson County, SE ¼ Sec. 22, T30S, R13E.	Percent composition	Percent basal area
Species:		
Aristida oligantha	31.8	2.01
Bouteloua curtipendula	15.8	.97
Bromus japonicus	.4	.3
Chloris verticillata	3.0	1.9
Eragrostis megastachya	.8	.6
Panicum virgatum	36.7	2.38
Paspalum pubiflorum	13.5	.89
Total	.....	6.53
AREA NO. 24. Grazed prairie in the Chautauqua Hills, Elk County, SE ¼ Sec. 1, T30S, R12E.	Percent composition	Percent basal area
Species:		
Andropogon saccharoides	.6	.05
Andropogon scoparius	1.3	.10
Bouteloua curtipendula	60.0	5.69
Bromus japonicus	4.4	.42
Chloris verticillata	10.0	9.50
Panicum virgatum	.7	.06
Sporobolus sp.	23.0	2.19
Total	.....	9.46
AREA NO. 26. Grazed prairie 5 miles west of the Chautauqua Hills, Elk County, SW ¼ Sec. 36, T29S, R11E.	Percent composition	Percent basal area
Species:		
Bouteloua curtipendula	52.0	3.91
Bromus japonicus	16.4	1.23
Panicum virgatum	30.0	2.22
Xanthocephalum dracunculoides	1.6	.13
Total	.....	7.50

TABLE 10. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 5.

AREA No. 20. Grazed prairie 2 miles east of the Chautauqua Hills, Wilson County, NE ¼ Sec. 15, T30S, R14E.	Percent composition	Percent basal area
Species:		
Aristida oligantha	24.4	1.64
Bromus japonicus	30.0	2.03
Chloris verticillata	14.0	.94
Lespedeza violacea	3.5	.27
Paspalum pubiflorum	11.5	.72
Panicum virgatum	14.3	.91
Solanum americanum	.6	.04
Solidago altissima	1.4	.12
Total	.....	6.67

AREA No. 10. Grazed prairie 10 miles north of the Chautauqua Hills, Woodson County, NE ¼ Sec. 24, T23S, R15E.	Percent composition	Percent basal area
Species:		
Aristida longespica	2.0	.14
Aristida oligantha	45.0	3.62
Bouteloua curtipendula	37.0	2.84
Bromus japonicus	16.0	1.14
Total	.....	6.90

AREA No. 15. Grazed prairie 8 miles east of the Chautauqua Hills, Woodson County, SW ¼ Sec. 26, T25S, R16E.	Percent composition	Percent basal area
Species:		
Bouteloua curtipendula	20.0	1.46
Bromus japonicus	13.0	1.03
Chloris verticillata	29.0	2.20
Croton monanthogynus	.7	.06
Paspalum ciliatifolium	33.5	2.60
Panicum virgatum	1.0	.08
Ruellia humilis	.6	.05
Vernonia baldwini v. *interior*	2.0	.18
Xanthocephalum dracunculoides	.2	.02
Total	.....	7.68

TABLE 10. Percentage Composition and Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 5.—*Concluded*

AREA NO. 5. Grazed prairie 1 mile west of the Chautauqua Hills, Chautauqua County, NW ¼ Sec. 4, T33S, R11E.	Percent composition	Percent basal area
Species:		
Andropogon saccharoides	10.0	.44
Aristica oligantha	30.0	1.28
Bouteloua curtipendula	52.0	2.30
Croton monanthogynus	.4	.02
Panicum dichotomiflorum	4.0	.17
Panicum lanuginosum	2.9	.12
Rubus parviflorus	.7	.03
Total	.....	4.36

TABLE 11. Percentage Composition of Basal Area of Grass Species and Forbs in Areas of Prairie Type No. 6.

AREA NO. 7. Grazed prairie in the Chautauqua Hills, Chautauqua County, SW ¼ Sec. 30, T33S, R12E.	Percent composition	Percent basal area
Species:		
Andropogon saccharoides	21.0	1.89
Bouteloua curtipendula	3.3	.28
Bromus secalinus	23.4	2.19
Buchloe dactyloides	10.0	.86
Chloris verticillata	34.0	2.69
Eragrostis capillaris	4.8	.41
Panicum virgatum	2.0	.18
Plantago aristata	1.5	.12
Total	.....	8.62

AREA NO. 17. Grazed prairie 5 miles west of the Chautauqua Hills, Greenwood County, NW ¼ Sec. 31, T25S, R13E.	Percent composition	Percent basal area
Species:		
Aristida oligantha	10.2	.71
Bromus japonicus	12.0	.85
Buchloe dactyloides	8.2	.56
Chloris verticillata	60.0	4.23
Eragrostis intermedia	5.8	.40
Paspalum ciliatifolium	3.0	.21
Total	.....	6.96

As the summer aspect sets in numerous plants go down, grasses start blooming, and there is a change to composites and other groups. Some of the more common plants found are *Teucrium canadense, Thelesperma trifidum, Ratibida columnifera, R. pinnata, Echinacea pallida, E. angustifolia, Salvia azurea* var. *grandiflora, Penstemon tubaeflorus, Coreopsis palmata, Dalea purpurea, Sckrankia nuttallii, Scutellaria parvula, Callirhoe alcaeoides,* and *Helianthus rigidus.*

In the fall the relatively good prairie areas are covered with tall grasses in which are dispersed scattered individuals or colonies of forbs. The most common of these are *Aster oblongifolius, A. patens, A. laevis, Helianthus tenellum, Vernonia fasciculata, Solidago altissima, Liatris punctata, L. asper, Kuhnia eupatoriodes* var. *corymbulosa,* and *Eupatorium altissimum.*

Flood plain woods: Most of the major stream courses (Map 2) are wooded along their banks and for varying distances out over the land which is subject to overflow, called the flood plain. These water courses have eroded through the sandstone of the uplands and have formed deep to shallow valleys. Limestone is commonly evident in exposed creek beds or on banks. Calcareous and alluvial soils are found in these low valleys. A wide variety of trees and shrubs are found in the flood plain woods (Plates 10 and 12; Fig. 2). In addition to the species included in Table 3, the following species of trees and shrubs are characteristic of the flood plains. *Aesculus glabra, Ceanothus americanus, Acer negundo, Populus deltoides, Euonymus atropurpureus, Fraxinus quadrangulata, F. americana, Cornus drummondi, Symphoricarpos orbiculatus,* and *Cercis canadensis.* A few of the common woody vines are *Smilax herbacea, S. tamnoides* var. *hispida, Vitis vulpina,* and *V. cinera.*

The characteristic species of the understory (Plate 10; Fig. 2) can be divided into seasonal aspects as follows: Spring—*Phlox divaricata* var. *laphamii, Mirabilis nyctaginea, Oxalis stricta, Carex bicknellii, C. davisii, C. gravida, Violo pensylvanica, Ruellia strepens, Stachys tenuifolia, Ellisia nyctelea, Tradescantia bracteata,* and *Lamium purpureum;* Summer—*Elymus virginicus, Asclepias stenophylla, Polygonum persicaria, P. punctatum, Sanicula canadensis, Geum canadensis* var. *camporum, Campanula americana,* and *Urtica gracilis;* Fall—*Uniola latifolia, Thalictrum dasycarpum, Verbesina virginica, Verbena urticifolia, Bidens polylepis, Eupatorium rugosa, Laportea canadensis,* and *Actinomeris alternifolia.*

Prairie woodlands: The prairie woodlands (Plate 11) are areas where there are stands of trees or scattered individuals intermixed

with prairie. This is common throughout the area. Species common to both prairie and open woodlands are found here.

Ponds and lakes: For the most part the ponds of the area are located in prairie pastures. The flora around many of the artificial ponds is the same as the surrounding area except for moist ground a few feet around the water's edge. Here are often found species of *Carex, Juncus, Eleocharis, Cyperus, Bacopa, Polygonum,* and *Veronica.* There are a few artificial lakes in both woodland (Plate 12; Fig. 1) and prairie areas. Depending on the habitat in which the lake was formed, their shores are variously wooded or treeless. The characteristic trees along shores of lakes in lowland areas are species of *Salix, Populus, Fraxinus, Ulmus, Acer,* and *Platanus.* The shores of lakes in upland areas are characteristically wooded with species of *Quercus, Ceanothus, Carya, Juglans, Celtis, Ptelea,* and others. In the shallow water and in moist places around lakes are found species of *Typha, Najas, Nelumbo, Rhamnus, Cephalanthus, Potamogeton,* and *Myriophyllum.* Farther away from the water are species of *Cyperus, Carex, Fimbristylis, Rumex, Polygonum, Ranunculus, Veronica* and *Echinochloa.*

Marshes: The marshes in the Chautauqua Hills are small bodies of water surrounded by soft wet land and usually are characterized by species of *Echinochloa, Amorpha, Carex, Poa, Juncus, Polygonum, Eleocharis, Cephalanthus, Lippia, Cyperus, Alisma, Jussiaea,* and *Sagittaria* growing along the margins. Plants found growing farther out in the water are species of *Typha, Myriophyllum, Utricularia, Lemna, Spirodela,* and *Elodea.*

Occasionally temporary water holes are formed in woodlands and prairie (Plate 14) after heavy rains and remain long enough for a few water plants to become established.

Gullies and Ravines: The gullies in the Chautauqua Hills are shallow to deep gorges excavated by running water, but through which water commonly runs only after rains. These occur in prairie and woodland. Some prairie gullies are variously wooded with *Quercus macrocarpa, Gleditsia triacanthos, Maclura pomifera, Prunus angustifolia, Ulmus rubra, U. americana, Morus rubra,* and others. Treeless prairie gullies may have various shrubs on the banks such as species of *Rosa, Rubus, Cornus, Rhamnus,* and *Ceanothus.* Other plants characteristic of prairie gullies are *Juncus torreyi Eleocharis calva, Cyperus esculentus, Erigeron philadelphicus, Oenothera serrulata, Arenaria patula, hypericum spaerocarpum, Justicia americana,* and *Amorpha fruticosa.*

Gullies in woodlands (Plates 15 and 16) characteristically support species common to the surrounding area plus numerous species also found in flood plains (Table 2). Other species common in wooded gullies are *Geum canadensis, Coreopsis palmata, Desmodium glutinosum, Bromus purgans, Mimulus alatus, Hypericum mutilum, Isanthus brachiatus,* and *Samolus parviflorus.* Several species of ferns are found along the rocky gully banks (Plates 17 and 18; Fig. 2). Some of the common species are *Woodsia obtusa, Dryopteris marginalis, Asplenium platyneuron, A. resiliens, A. trichomanes, Cystopteris fragilis* and varieties, *Onoclea sensibilis, Pellaea atropurpurea,* and *P. glabella.*

Ravines resemble gullies except that they are larger and have been eroded deeper. Like gullies, ravines may have temporary streams (Plates 19; Fig. 1). The characteristic trees (Table 5) and other plants are essentially the same as for gullies. However, a few additional species, such as *Pellaea dealbata* will be present in areas where limestone cliffs are exposed due to past erosion. Also *Aquilegia canadensis* var. *latiuscula* is more common on sheer ravine cliffs.

Invaded woodlands: In cultivated and disturbed areas there are places where certain trees have become established since settlement. These trees are common along borders of some fields, roadsides, in wasteland, and in some overgrazed pastures. Some of the characteristic trees and shrubs in these places are *Maclura pomifera, Gleditsia triacanthos, Populus alba, Robinia pseudo-acacia, Catalpa speciosa, Morus alba, M. rubra, Acer negundo, Prunus americana, P. serotina, Rosa arkansana* var. *suffulta, R. setigera,* and *Cornus drummondi.*

Species found in the understory of such woodlands are, among others, *Ipomoea hederacea, Impatiens pallida, Thlaspi arvensis, Hemerocallis fulva,* and *Arisaema dracontium.*

Roadside plants: Roadside vegetation consists essentially of the border plants of whatever plant community the road passes (Plate 20). Temporary water holes in roadside ditches may support marsh plants for a time. Roadsides also provide a habitat for some annual weeds. A few plants, which have escaped and become established along roadsides are species of *Delphinium, Hemerocallis, Lespedeza, Melilotus,* and *Saponaria.* Common along roadsides in summer and fall are species of *Helianthus, Sehrankia, Silphium, Verbena,* and *Liatris.*

Cultivated fields: These fields are usually invaded by a number

of plants commonly called weeds. They are mostly annuals and grow in such large numbers that they cannot always be destroyed, thus they are usually maintained in the habitat by seed. A few of the most common plants are species of *Lactuca, Echinochloa, Ipomoea, Thlaspi, Bromus, Amaranthus, Chenopodium, Helianthus, Solanum, Aster, Conyza, Lepidium, Paspalum,* and *Physalis.*

Abandoned fields: Fields which have been plowed and then left idle are quickly invaded by weeds and grasses. Characteristic grasses are species of *Aristida, Eragrostis, Bromus, Agrostis, Chloris, Digitaria,* and *Panicum.* Weeds common in cultivated fields are found here also.

RELATIONSHIP OF THE CHAUTAUQUA HILLS FLORA TO THAT OF ADJACENT AREAS

The Chautauqua Hills physiographic province in Kansas actually is a northern extension of the Texan Biotic Province. The area is bordered on the north by the Illinoian Biotic Province. From the east there is an influx from the Carolinian and on the west from the Kansan Biotic Provinces. Dice (1943) truncated the Texan Biotic Province on the north at the Oklahoma border along the area of the southern boundary of the Chautauqua Hills in Kansas. As a result of this study, however, the writer is convinced that the northern boundary of the Texan Biotic Province should be extended to include the Chautauqua Hills of Kansas.

The vegetation of the Chautauqua Hills, while it does have some areas of tall grass and mixed forests, is primarily that of an oak savanna which is very similar to the oak-hickory savanna of the Texan Biotic Province. The characteristic trees of the oak savanna in the Chautauqua Hills are *Quercus stellata* and *Q. marilandica.* Dyksterhuis (1948) lists the above species as the main trees in open, savanna-like stands, known as Cross Timbers, in the Texas and Oklahoma area of the Texan Biotic Province. Rice and Penfound (1956) list *Quercus stellata* and *Q. marilandica* as dominants in the deciduous forest frontier in Oklahoma which is located in the Texan Biotic Province. Dice (1943) states that trees of the Texan Biotic Province are chiefly oaks and hickories, of which the most important are *Quercus stellata, Q. marilandica,* and *Carya texana.* The latter species is reported for the Chautauqua Hills but essentially it is replaced in this area by *Carya cordiformis* and to some extent by *C. ovata.*

Blair (1950) in discussing the Texan Biotic Province in Texas states that the sandy soils support an oak-hickory forest in which

the principal dominants are *Quercus stellata, Q. marilandica,* and *Carya texana.* The Texan Biotic Province in Oklahoma includes parts of a *Stipa-Koeleria* Association and *Andropogon* Associes. The major part of it, however, consists of an oak-hickory savanna. This area is characterized by Bruner (1931) as ". . . a scrubby growth of oaks usually associated with hickory. Grassland alternating with limited areas of open woodland is characteristic of the northern and southern extremities, while throughout the central part the woodland dominates and grassy areas occur only locally . . . The rocky slopes are clothed by forests which are mostly of the blackjack-post oak type. On the steep, most exposed places, cedar (*Juniperus virginiana*) and sumac (*Rhus glabra*) abound. The following are dominant: *Quercus marilandica, Q. stellata,* and *Carya texana.*" *Juniperus virginiana* and *Rhus glabra* are also characteristic of the Chautauqua Hills flora. Study of the main characteristic trees of the Texan Biotic Province impressed the writer with the fact that they are essentially the same as for the Chautauqua Hills area. Several other species characteristic of the Texan Biotic Province are found in the Chautauqua Hills, thus showing a further influence on the flora of that area. A few of these species are *Andropogon scoparius, A. saccharoides, Agropyron smithii, Scutellaria parvula, Sanicula canadensis, Selenia aurea, Ruellia strepens, Caradamine parviflora, Plantago virginica, Mollugo verticillata, Buchnera americana, Hypericum punctatum, Stylosanthes biflora, Strophostyles helvola, Chrysopsis pilosa, Gymnopogon ambiguus, Gnaphalium purpureum, Parietaria pennsylvanica, Aster patens, Solidago ulmifolia, Lespedeza stuvei, Vernonia fasciculata, Helenium autumnale, Diodia teres, Lechea tenuifolia, Bromus purgans, Eleusine indica, Muhlenbergia schreberi, M. sobolifera, Panicum lanuginosum, Sporobolus neglectus,* and *Uniola latifolia.*

Several species in the southern part of the Texan Biotic Province which are not found in the Chautauqua Hills are replaced there by different species of the same genera occurring in the province. Some examples are as follows: *Ranunculus hispidus* in the southern part of the Texan Biotic Province is replaced in the Chautauqua Hills by *R. fascicularis; Lithospermum carolinense* is replaced by *L. incisum; Stipa leucotricha* is replaced by *S. spartea; Tradescantia reflexa* is replaced by *T. ohiensis; Crotalaria rotundifolia* is replaced by *C. sagittalis; Portulaca pilosa* is replaced by *P. parvula; Eragrostis hirsuta* is replaced by *E. megastachya.*

Due to the fact that the oak savanna, which makes up the conspicuous vegetation of the Chautauqua Hills, is essentially similar

to the oak-hickory savanna of the Texan Biotic Province and that many species making up the flora of the Chautauqua Hills represent a strong influence from the above province, the Chautauqua Hills of Kansas should be included in the Texan Biotic Province.

The influence of other surrounding biotic provinces on the flora of the Chautauqua Hills is very little compared to that of the Texan.

The influence on the flora of the Chautauqua Hills from the Illinoian Biotic Province is to be found primarily along streams, flood plains, and moist hillsides. Species are found here which are common to the above biotic province. They are species of *Ulmus* and *Aesculus* as well as *Platanus occidentalis, Quercus macrocarpa, Populus deltoides, Celtis occidentalis,* and *Cercis canadensis.*

The Kansas Biotic Province has very little influence on the flora of the Chautauqua Hills, but a few species which do represent a Kansan influence are *Bouteloua gracilis, B. hirsuta, Buchloe dactyloides, Sporobolus cryptandrus, Koeleria cristata, Festuca octoflora, Hordeum pusillum, Kuhnia eupatorioides, Monolepis nuttaliana, Castilleja sessiliflora, Plantago purshii, Oxalis stricta,* and *Hedeoma hispida.*

Hardwood forest richly diversified in tree species is characteristic of the Carolinian Biotic Province. The forests over most of the Chautauqua Hills are characterized by relative few different species of oak. However, mixed forests do occur on some moist hillsides and along streams, indicating a small influence from the Carolinian. A few species in the area which represent an influence from this province are *Hexalectris spicata, Viburnum rufidulum,* and *Yucca glauca* var. *mollis.*

There are no endemic species present in the Chautauqua Hills. The flora of the area is influenced by the surrounding Kansas, Illinoian, Carolinian, and Texan Biotic Provinces, but at least 90 per cent of this influence is from the latter province of which it actually is a part.

ANNOTATED LIST

The following list includes all the species, subspecies, varieties, and forms of ferns and flowering plants found in the Chautauqua Hills area. It also includes species which were not found, but for which specimens are on file, from the area, in the Herbarium at the University of Kansas. These records are so designated in the list by the name and number or date of the collector placed with the species concerned. Several species are also included on the authority of Gates (1940). In the latter cases species involved are designated by Gates (1940) being placed after the species concerned.

The habitat of each species, and the counties in which it was found are included, except that the habitat is not given for species included on the authority of Gates (1940). With the latter exception, county distribution of species is based solely on field observation and herbarium records. Where no county is listed after a species, that particular taxon is found in all the counties of the Chautauqua Hills area.

The listing of families follows that of Gray's Manual of Botany, 8th Edition. The genera and species are listed alphabetically within the family. The nomenclature follows that of Gray's Manual of Botany 8th Edition insofar as it applies to this area.

SELAGINELLACEAE

Selaginella rupestris (L.) Spring: On shallow soil over sandstone outcrops and on sandy banks of gullies in upland woods.

ISOETACEAE

Isoetes melanopoda Gay and Durieu.: On shallow soil, over limestone, in a small prairie gully. Found once by R. L. McGregor 10861, three miles west of Neodesha, Wilson County.

Isoetes melanopoda Gay and Durieu., forma *pallida* (Engelm.) Fern.: On shallow soil, over limestone, in a small prairie gully. Found once by R. L. McGregor 10267, three miles west of Neodesha, Wilson County.

EQUISETACEAE

Equisetum arvensis L.: On sandy soil of a wooded cliff. Found once, nine miles southwest of Yates Center, Woodson County.

Equisetum hiemale L., var. *elatum* (Engelm.) Morton: In sandy soil of wooded gullies in uplands. All counties except Montgomery and Wilson.

Equisetum laevigatum A. Br.: On wet banks of streams. Collection by W. H. Horr, Sept. 1, 1930, Woodson County.

OPHIOGLOSSACEAE

Botrychium virginianum (L.) SW.: In moist woods, thickets, and in shallow soil over limestone of a wooded hillside. Collections by P. H. Humfeld 842, Chautauqua County; 801, Greenwood County; W. H. Horr, June 28, 1930, Greenwood County.

Ophioglossum engelmanni Prantl.: On rocky open wooded slopes, and rocky prairie hillsides. Collections by R. L. McGregor 4186, Chautauqua County; 10734, Elk County; P. H. Humfeld 107, Montgomery County; 123, Wilson County.

POLYPODIACEAE

Adiantum pedatum L.: In shallow soil over sandstone outcrops of wooded gullies in uplands. Collection by R. L. McGregor 917, Woodson County.

Asplenium platyneuron (L.) Oakes: In crevices of sandstone and limestone outcrops of wooded gullies and slopes.

Asplenium platyneuron (L.) Oakes, forma *serratum* (E. S. Miller) Hoffm.: In shallow soil over sandstone outcrops of a moist gully in upland woods. Found once, three miles southeast of Yates Center, Woodson County.

Asplenium resiliens Kunze: In crevices of sandstone and limestone outcrops of wooded gullies.

Asplenium trichomanes L.: In crevices of sandstone outcrops of open scrub oak wooded hillsides. All counties except Montgomery and Wilson.

Camptosorus rhizophyllus (L.) Link: On calcareous soil, and in crevices of wooded limestone escarpments.

Cheilanthes feei Moore: In crevices of limestone outcrops on wooded slopes. Found once, ten miles southwest of Sedan, Chautauqua County.

Cheilanthes lanosa (Michx.) D. C. Eaton: In crevices of sandstone outcrops of upland wooded slopes.

Cystopteris fragilis (L.) Bernh., var. *protrusa* Weath.: In shallow soil over sandstone outcrops of upland wooded gullies. Chautauqua and Greenwood counties.

Cystopteris fragilis (L.) Bernh., var. *simulans* (Weath.) McGregor: In crevices of limestone and sandstone outcrops of wooded slopes. All counties except Elk.

Cystopteris fragilis (L.) Bernh., var. *tennesseensis* (Shaver) McGregor: In crevices of limestone and sandstone outcrops in woodlands.

Dryopteris marginalis (L.) Gray: In rock crevices of upland hillsides and prairie gullies. Frequent.

Onoclea sensibilis L.: On moist wooded creek and stream banks. All counties except Greenwood and Wilson.

Onoclea sensibilis L., forma *obtusilobata* (Schkuhr) Gilbert: On moist wooded creek banks. Collections by R. L. McGregor 2392, Montgomery County; 2411, Woodson County.

Pellaea atropurpurea (L.) Link: In crevices of limestone and sandstone outcrops of wooded hillsides. All counties except Elk.

Pellaea dealbata (Pursh) Prantl.: In crevices of limestone outcrops of wooded gullies. All counties except Elk.

Pellaea glabella Mett.: In shallow soil and in crevices of limestone and sandstone outcrops of wooded slopes. All counties except Elk.

Polypodium polypodioides (L.) Watt., var. *michauxianum* Weath.: In crevices and on sides of sandstone outcrops in a wooded upland gully. Collected in one location two miles northeast of Sedan, Chautauqua County by P. H. Humfeld 357, 808; R. L. McGregor 3379.

Polystichum acrostichoides (Michx.) Schott.: In slightly eroded gulches of wooded hillsides. All counties except Elk.

Thelypteris palustris Schott., var. *pubescens* (Lawson) Fern.: In sandy soil of wooded hillsides. All counties except Greenwood.

Woodsia obtusa (Spreng.) Torr.: In moist upland woods. Frequent.

CUPRESSACEAE

Juniperus virginiana L.: Hilltops and slopes of rocky open woods.

TYPHACEAE

Typha latifolia L.: Growing in dense stands at edges of lakes and marshes. Woodson, Greenwood, and Montgomery counties.

ZOSTERACEAE

Potamogeton crispus L.: In shallow water of Lake Fegan. Woodson County.

Potamogeton diversifolius Raf.: In ponds and streams. Collections by P. A. Rydberg and R. Imler 414, Montgomery County; R. L. McGregor 3203, Woodson County; R. H. Thompson, June 8, 1949, Wilson County.

Potomogeton foliosus Raf.: In shallow streams and lakes. Greenwood and Woodson counties.

Potomogeton gramineus L.: In marshes and streams. Woodson County.

Potamogeton nodosus Poir.: Along the shore of Lake Fegan and in streams of wooded valleys. Elk and Woodson Counties.

NAJADACEAE

Najas guadalupensis (Spreng.) Magnus: In water along the shore of Lake Fegan. Woodson County.

ALISMACEAE

Alisma subcordatum Raf.: In marshes and in shallow standing water of waste places. Woodson County.

Echinodorus cordifolius (L.) Griseb.: Reported for Wilson County, Gates (1940).

Lophotocarpus calycinus (Engelm.) J. C. Smith: Reported for Woodson County, Gates (1940).

Sagittaria ambigua J. H. Smith: In a shallow water hole of a prairie pasture. Collection by P. A. Rydberg and R. Imler 402, Montgomery County.

Sagittaria latifolia Willd., var. *latifolia:* Borders of lakes and marshes, and in wet roadside ditches. Chautauqua, Montgomery, and Woodson Counties.

Sagittaria latifolia Willd., var. *obtusa* (Muhl.) Wieg.: Reported for Chautauqua County, Gates (1940).

HYDROCHARTACEAE

Elodea canadensis Michx.: In marshes and in water holes in prairie pastures and woodlands. Woodson County.

GRAMINEAE

Aegilops cylindrica Host.: In a roadside ditch bordering a prairie pasture. Found once, in Woodson County.

Agropyron smithii Rydb.: In overgrazed pastures and waste places. Elk, Greenwood, and Woodson counties.

Agrostis alba L.: In waste fields and disturbed areas of prairie pastures. Woodson County.

Agrostis elliottiana Schultes: Reported for Chautauqua County, Gates (1940).

Agrostis hiemalis (Walt.) BSP.: In sandy soil of open wooded hillsides. Woodson County.

Agrostis scabra Willd.: In sandy soil of prairie hay fields and open upland woods. Woodson County.

Alopecurus carolinianus Walt.: Reported for Chautauqua County, Gates (1940).

Andropogon gerardi Vitman: Lower slopes of prairie hay fields and pastures, and prairie openings in woods. Frequent.

Andropogon saccharoides Sw.: In prairie hay fields, pastures, and prairie woodlands.

Andropogon scoparius Michx., var. *scoparius* Prairie hay fields, pastures, and prairie woodlands. Frequent.

Andropogon scoparius Michx., var. *neo-mexicanus* (Nash) Hitchc.: In a rocky prairie pasture. Collection by R. L. McGregor 9807, Greenwood County.

Andropogon ternarius Michx.: Reported for Wilson County, Gates (1940).

Andropogon virginicus L.: Rocky scrub oak wooded hillside. Collection by R. L. McGregor 4181, Chautauqua County.

Aristida basiramea Engelm.: Overgrazed prairie pastures and waste places. Collection by B. L. Wagenknecht 1724, Montgomery County.

Aristida dichotoma Michx.: Upland prairies and on sandy soil of open scrub oak woods. Montgomery, Wilson, and Woodson counties.

Aristida intermedia Scribn. and Ball: Sandy soil of open rocky upland woods. Wilson and Woodson counties.

Aristida longespica Poir.: In calcareous soil of a prairie pasture and in sandy soil of open scrub oak woods. Rare. Montgomery and Woodson counties.

Aristida oligantha Michx.: In overgrazed prairie pastures and open woods.

Aristida purpurascens Poir.: In sandy soil of open wooded slopes. Chautauqua, Montgomery, and Woodson counties.

Bouteloua gracilis (KBK.) Lag.: Reported for Greenwood and Woodson counties, Gates (1940).

Bouteloua hirsuta Lag.: In overgrazed prairie pastures and open grazed woods. Chautauqua, Montgomery, and Woodson counties.

Bromus commutatus Schrad.: Eroded areas in sandy prairie pastures. Collections by R. L. McGregor 10319, Greenwood County; 10190, Montgomery County.

Bromus inermis Leyss.: Fields, waste places, and overgrazed pastures. Woodson County.

Bromus japonicus Thunb.: Overgrazed prairie pastures and fields.

Bromus purgans L.: Prairie pasture gullies and open woods. Greenwood and Woodson counties.

Bromus racemosus L.: Fields and waste places. Collections by W. H. Horr, July 11, 1930, Woodson County; July 12, 1930, Wilson County.

Bromus secalinus L.: Overgrazed prairie pastures and open sandy woods.

Bromus tectorus L.: Low prairie hay fields and pastures. Montgomery and Woodson counties.

Buchloe dactyloides (Nutt.) Engelm.: Dry overgrazed prairie pastures. Greenwood and Woodson counties.

Cenchrus longispinus (Hack.) Fern.: Roadsides, waste places, and disturbed pastures. All counties except Elk and Wilson.

Chloris verticillata Nutt.: Waste places and overgrazed prairie pastures.

Cinna arundinacea L.: In sandy soil of an open wooded gully. Woodson County.

Danthonia spicata (L.) Beauv., var. *longipila* Scribn. and Merr.: Sandy soil of an open scrub oak woods. Rare. Collected at Woodson County State Park, Woodson County.

Digitaria sanguinalis (L.) Scop.: Waste places, fields, and overgrazed pastures.

Diplachne acuminata Nash.: Reported for Greenwood County, Gates (1940).

Echinochloa crusgalli (L.) Beauv.: On banks of drainage ditches in fields and roadsides.

Echinochloa pungens (Poir.) Rydb., var. *pungens:* Roadside waste places and fields. Woodson County.

Echinochloa pungens (Poir.) Rydb., var. *microstachya* (Wieg.) Fern. and Grisc.: Moist waste places and on banks of streams in open woods. Montgomery and Woodson counties.

Eleusine indica (L.) Gaertn.: Reported of all counties except Greenwood and Wilson, Gates (1940).

Elymus canadensis L., var. *canadensis:* Prairie hay fields and pastures. Chautauqua, Elk, and Woodson counties.

Elymus canadensis L., var. *canadensis,* forma *glaucifolius* (Muhl.) Fern.: Prairie hay fields and pastures. Chautauqua and Woodson counties.

Elymus villosus Muhl.: On creek banks and in low woods. Collection by R. L. McGregor 10819, Montgomery County.

Elymus villosus Muhl., forma *arkansanus* (Scribn. and Ball) Fern. Reported for Greenwood County, Gates (1940).

Elymus virginicus L., var. *virginicus:* In prairie pastures and borders of woods.

Elymus virginicus L., var. *virginicus,* forma *hirsutiglumis* (Scribn.) Fern.: In sandy soil of an upland woods. Collected once, in Woodson County.

Elymus virginicus L., var. *glabrifolius* (Vasey) Bush: In upland woods bordered by prairie. Wilson and Woodson Counties.

Elymus virginicus L., var. *submuticus* Hook: Reported for Chautauqua and Greenwood counties, Gates (1940).

Eragrostis capillaris (L.) Nees: In sandy soil of open grazed upland woods and prairie pastures.

Eragrostis intermedia Hitch.: In prairie hay fields and pastures.

Eragrostis megastachya (Koel.) Link.: Overgrazed pastures and waste places.

Eragrostis pectinacea (Michx.) Scribn.: Rocky prairie pastures and waste places. All counties except Elk and Greenwood.

Eragrostis poaeoides Beauv. ex-Roem. and Schult.: Sandy soil of a dry lake bed. Reported for Woodson County, McGregor and Volle (1950).

Eragrostis reptans (Michx.) Nees: Reported for Chautauqua County, Gates (1940).

Eragrostis spectabilis (Pursh) Steud.: Fields and roadsides. Collection by W. H. Horr, July 10, 1930, Woodson County.

Eriochloa contracta Hitchc.: Reported for all counties except Wilson, Gates (1940).

Festuca elatior L.: Low prairie pastures and waste places. Collection by W. H. Horr 207-1, Wilson County.

Festuca octoflora Walt.: In moist grassy meadows. Woodson County.

Festuca ovina L.: In sandy soil of open scrub oak woods. Chautauqua and Woodson counties.

Festuca paradoxa Desv.: Roadsides and railroad embankments. Woodson County.

Glyceria striata (Lam.) Hitchc.: In moist shaded woods. Woodson County.

Gymnopogon ambiguus (Michx.) BSP.: In sandy soil of open upland woods. Found twice, in Chautauqua and Montgomery counties.

Hordeum pusillum Nutt.: Rocky prairie pastures, wooded gullies, and clearings in woods. Greenwood, Montgomery, and Woodson counties.

Koeleria cristata (L.) Pers.: In prairie and open ground. Collections by W. H. Horr, July 5, 1930, Montgomery County; R. L. McGregor 3163, Woodson County; 10273, Wilson County.

Leersia oryzoides (L.) Sw.: Sandy soil of open scrub oak woods, Montgomery and Woodson counties.

Leersia virginica Willd.: Moist woods. Collection by B. L. Wagenknecht 1772, Chautauqua County.

Leptochloa filiformis (Lam.) Beauv.: On an alluvial deposit near Fall River. Collection by R. L. McGregor 5736, Wilson County.

Leptoloma cognatum (Schultes) Chase: Sandy prairie pastures. Woodson County.

Lolium perenne L.: Reported for Montgomery County, Gates (1940).

Melica nitens (Scribn.) Nutt.: In open flood plain woods of Fall River. Collected once, in Greenwood County.

Melica porteri Scribn.: Reported for Montgomery County, Gates (1940).

Muhlenbergia brachyphylla Bush: In creek valley woods. Collection by B. L. Wagenknecht 1695, Montgomery County.

Muhlenbergia capillaris (Lam.) Trin.: In sandy soil of open wooded hillsides. Montgomery and Wilson counties.

Muhlenbergia cuspidata (Torr.) Nash: In sandy soil of a rocky upland wooded hillside. Collection by R. L. McGregor 9800, Greenwood County.

Muhlenbergia frondosa (Poir.) Fern.: Creek banks and wooded gullies. Chautauqua County.

Muhlenbergia mexicana (L.) Trin.: Reported for Elk County, Gates (1940).

Muhlenbergia racemosa (Michx.) BSP.: Creek valley woods and upland wooded gullies. Chautauqua, Wilson, and Woodson counties.

Muhlenbergia schreberi J. F. Gmel.: Wooded prairie gullies and on a rocky wooded cliff. Woodson County.

Muhlenbergia sobolifera (Muhl.) Trin.: In sandy soil of an open wooded gully in upland. Found once, in Woodson County.

Panicum agrostoides Spreng.: On sandy open wooded slopes. Montgomery County.

Panicum boscii Poir.: In shallow soil of a wooded limestone escarpment. Collection by R. L. McGregor 3398, Montgomery County.

Panicum capillare L.: Eroded pastures and waste places. Montgomery and Woodson counties.

Panicum clandestinum L.: In sandy soil of a shaded bank in an open oak woods. Collection by R. L. McGregor 10850, Montgomery County.

Panicum dichotomiflorum Michx.: In prairie hay fields and good grazed pastures.

Panicum lanuginosum Ell., var. *fasciculatum* (Torr.) Fern.: Moist low woods and wooded upland gullies. Chautauqua County.

Panicum lanuginosum Ell., var. *lindheimeri* (Nash) Fern.: In shallow soil over sandstone outcrops of an oak wooded cliff. Collected once, in Woodson County.

Panicum leibergii (Vasey) Scribn.: Reported for Montgomery County, Gates (1940).

Panicum oligosanthes Schultes, var. *helleri* (Nash.) Fern.: Low prairie pastures and at borders of woods. Montgomery and Woodson counties.

Panicum oligosanthes Schultes, var. *scribnerianum* (Nash) Fern.: Reported for all counties except Elk and Woodson, Gates (1940).

Panicum praecocius Hitchc. and Chase: Reported for Greenwood County, Gates (1940).

Panicum spaerocarpon Ell.: In sandy soil of open upland woods. Montgomery, Wilson, and Woodson counties.

Panicum virgatum L.: Prairie hay fields, pastures, and in open flats surrounded by woods. Frequent.

Paspalum ciliatifolium Michx., var. *ciliatifolium:* Prairie hay fields, pastures, and open woods. Montgomery and Woodson counties.

Paspalum ciliatifolium Michx., var. *muhlenbergii* (Nash) Fern.: Rocky prairie pastures and rocky flats surrounded by woods.

Paspalum fluitans (Ell.) Kunth.: On mud banks and extending out on surface of water in streams. Collections by W. H. Horr E173, Wilson County; R. L. McGregor 5731, Wilson County.

Paspalum pubiflorum Rupr., var. *glabrum* Vasey: Low prairie hay fields and pastures. Wilson and Woodson counties.

Phlaris canariensis L.: Low rocky prairie pastures. Collections by R. L. McGregor 10200, Montgomery County; 10247, Wilson County.

Phlaris caroliniana Walt.: Low prairie hay fields and pastures. Montgomery and Woodson counties.

Phleum pratense L.: Reported for Woodson and Montgomery counties, Gates (1940).

Poa annua L.: Reported for Chautauqua and Montgomery counties, Gates (1940).

Poa compressa L.: In a moist gulch of a prairie pasture. Found once, in Woodson County.

Poa pratensis L.: On banks of gullies in prairie pastures. Woodson County.

Poa sylvestris A. Gray: Reported for Montgomery County, Gates (1940.)

Schedonnardus paniculatus (Nutt.) Trel.: Prairie pastures, roadsides, and fields. Greenwood, Montgomery and Woodson counties.

Setaria faberii Herrm.: Roadsides and fields.

Setaria geniculata (Lam.) Beauv.: Roadsides, fields, and waste places.

Setaria glauca (L.) Beauv.: Overgrazed pastures, fields, and roadsides. Frequent.

Setaria viridis (L.) Beauv.: Overgrazed pastures and waste places.

Sorghastrum nutans (L.) Nash.: Low prairie hay fields and pastures.

Sorghum halepense (L.) Pers.: Fields and waste places.

Spartina pectinata Link: Low prairie hay fields and pastures.

Sphenopholis obtusata (Michx.) Scrib.: Prairie pastures, and prairie woodlands.

Sporobolus asper (Michx.) Kunth.: Rocky prairie hillsides and open woodlands.

Sporobolus pyramidatus (Lam.) Hitchc.: In sandy soil of an overgrazed prairie pasture. Found once, two miles northeast of Sedan, Chautauqua County.

Sporobolus vaginiflorus (Torr.) Wood.: Reported for Wilson County, Gates (1940).

Stipa spartea Trin.: On lower slopes of grazed and ungrazed prairies. All counties except Chautauqua.

Triodia elongata (Buckl.) Scribn.: In calcareous soil of a prairie pasture. Found once, seven miles northeast of Elk City, Montgomery County.

Triodia flava (L.) Smyth: Roadsides, waste places, and overgrazed pastures. Frequent.

Triodia flava (L.) Smyth, forma *cuprea* (Jacq.) Fosberg: In sandy soil along the edge of an open oak woods. Found once, in Woodson County.

Triodia stricta (Nutt.) Benth.: Reported for Montgomery County, Gates (1940).

Tripsacum dactyloides L.: Low grazed and ungrazed prairies, and roadsides.

Uniola latifolia Michx.: Flood plain woods and wooded gullies in upland.

CYPERACEAE

Bulbostylis capillaris (L.) C. B. Clark, var. *crebra* Fern.: Dry exposed lake bed and dry sandy soil of a prairie pasture. Collections by R. L. McGregor 3179, Woodson County; B. L. Wagenknecht 1714, Montgomery County.

Carex amphibola Steud., var. *turgida* Fern.: Reported for Montgomery County, Gates (1940).

Carex artitecta Mack.: Reported for Montgomery County, Gates (1940).

Carex bicknellii Britton: Prairie pastures and open woodlands. Woodson County.

Carex blanda Dewey: Wooded prairie gullies and flood plain woods. Woodson County.

Carex brevior (Dewey) Mackenz.: In low prairies and woods. Woodson County.

Carex bushii Mackenzie: In prairies and mud banks of water holes. Woodson County.

Carex davisii Schwein. and Torr.: On creek banks and in low woodlands. Woodson County.

Carex frankii Kunth: On a creek bank and along the shore of a marsh. Collections by W. H. Horr, July 5, 1930, Montgomery County; July 12, 1930, Wilson County.

Carex gravida Bailey, var. *gravida:* In low prairies and woods, and on banks of streams.

Carex gravida Bailey, var. *lunelliana* (Mack.) F. J. Herm.: Low prairies, woodlands, and on banks of streams. Woodson County.

Carex lanuginosa Michx.: Reported for Montgomery County, Gates (1940).

Carex leavenworthii Dewey: Reported for Chautauqua County, Gates (1940).

Carex lupulina Muhl.: Open woodlands and in gullies of prairie pastures. Woodson County.

Carex meadii Dewey: Low woodland prairies. Wilson and Woodson counties.

Carex microdonta Torr. and Hook.: Reported for Chautauqua and Montgomery counties, Gates (1940).

Carex vulpinoides Michx.: Reported for Greenwood County, Gates (1940).

Cyperus acuminatus Torr. and Hook.: On banks of ponds and marshes. Montgomery and Woodson counties.

Cyperus diandrus Torr.: In sandy soil of an exposed lake bed. Reported for Woodson County, McGregor and Volle (1950).

Cyperus erythrorhizos Muhl.: In sandy soil of an exposed lake bed. Collection by R. L. McGregor 4108, Woodson County.

Cyperus esculentus L.: Moist prairie gullies. Woodson County.

Cyperus ferruginescens Boeckl.: Reported for Elk, Montgomery, and Woodson counties, Gates (1940).

Cyperus filiculmis Vahl.: Prairie pasture gullies and open woodlands.

Cyperus inflexus Muhl.: Prairie gullies, open woodlands, and waste places. Woodson County.

Cyperus globulosus Aubl., var. *robustus* (Boeckl.) Shinners: Open wooded hillsides and along banks of water holes.

Cyperus setigerus Torr. and Hook.: Bank of a water hole in a prairie pasture. Collection by P. A. Rydberg and R. Imler 368, Montgomery County.

Cyperus strigosus L.: On bank of a creek. Collection by W. H. Horr, July 5, 1930, Montgomery County.

Eleocharis acicularis R. and S.: Open woods and low waste places. Woodson County.

Eleocharis calva Torr.: Marshes and prairie pasture gullies. Greenwood and Woodson counties.

Eleocharis compressa Sulliv.: Reported for Geenwood County, Gates (1940).

Eleocharis engelmanni Stued.: Low prairie pastures and wooded gullies. Woodson County.

Eleocharis macrostachya Britton: Along the edges of pasture ponds.

Eleocharis obtusa (Willd.) Schultes: Border of ponds and marshes, and moist prairie gullies.

Fimbristylis autumnalis (L.) R. and S., var. *mucronulata* (Michx.) Fern.: In moist sand of an exposed lake bed. Collection by R. L. McGregor 4094, Woodson County.

Fimbristylis baldwiniana (Schultes) Torr.: Muddy edge of a slough in a prairie pasture, and in moist sand of a slight depression on a wooded hillside. Collections by R. L. McGregor 4403, Chautauqua County; B. L. Wagenknecht 2265, Wilson County.

Fimbristylis caroliniana (Lam.) Fern.: In a low moist prairie pasture. Collection by R. L. McGregor 4316, Montgomery County.

Fimbristylis interior Britton: Sandy soil of a bluestem prairie. Collection by R. L. McGregor 10211, Montgomery County.

Scirpus atrovirens Muhl.: Banks of prairie ponds and in wet roadside ditches. Woodson County.

Scirpus fluviatilis (Torr.) Gray: Reported for Wilson County, Gates (1940).

Scirpus lineatus Michx.: In moist prairie pasture gulches. Collections by R. L. McGregor 10325, Greenwood County; 4318, Montgomery County; 10246, Wilson County.

Scirpus validus Vahl., var. *creber* Fern.: Reported for Wilson County, Gates (1940).

Scleria pauciflora Muhl.: In sandy soil of an open oak woods. Collection by R. L. McGregor 3186, Woodson County.

Scleria triglomerata Michx.: Prairie hay fields and roadsides. Collections by R. L. McGregor 4312, Montgomery County; W. H. Horr, July 5, 1930, Montgomery County.

ARACEAE

Arisaema dracontium (L.) Schott.

LEMNACEAE

Lemna minor L.: Stagnant pond. Collection by R. L. McGregor 2410, Wilson County.

Lemna perpusilla Torr.: Woodland marsh. Collection by W. H. Horr, July 11, 1930. Woodson County.

Spirodela polyrhiza (L.) Schleid.: In marshes and prairie water holes. Woodson County.

COMMELINACEAE

Commelina communis L.: Borders of creek woods, banks of ditches and fields.

Commelina virginica L.: Low woods, thickets, and roadsides. Collections by W. H. Horr, July 5, 1930, Chautauqua County; June 28, 1930, Greenwood County; July 12, 1930, Wilson County.

Tradescantia bracteata Small: Gullies in prairie pastures, creek banks, and borders of low woods.

Tradescantia ohiensis Raf.: Woodland borders, ditch banks, and fields.

JUNCACEAE

Juncus biflorus Ell.: Open woods and moist prairie gullies. Woodson County.

Juncus diffusissimus Buckl.: Open woodland and in sandy soil of an exposed lake bed. Collection by P. A. Rydberg and R. Imler 450, Montgomery County. Reported for Woodson County, McGregor and Volle (1950).

Juncus dudleyi Wieg.: Low moist prairie pasture. Collection by P. A. Rydberg and R. Imler 450a, Montgomery County.

Juncus interior Wieg.: Low prairies and open woodlands. Frequent.

Juncus kansanus F. J. Herm.: Reported for Chautauqua County, Gates (1940).

Juncus marginatus Rostk., var. *marginatus*: Along the borders of ponds and marshes, and on muddy banks of prairie gullies. Elk, Montgomery, and Woodson counties.

Juncus marginatus Rostk., var. *setosus* Coville: In sandy soil of open woods. Collected twice in Woodson County.

Juncus nodatus Coville: Muddy bank of a run-off stream in a prairie pasture. Collection by W. H. Horr, July 5, 1930, Chautauqua County.

Juncus tenuis Willd., var. *multicornis* E. Mey.: Low moist woods, marshes, and along banks of standing water in prairie gullies. Woodson County.

Juncus torreyi Coville: In alluvial soil of flood plain woods, prairie gullies, and along borders of fields.

LILIACEAE

Allium canadense L., var. *canadense*: Prairies, roadsides, and exposed slopes.

Allium canadense L., var. *fraseri* Ownby: Prairie pastures, roadsides, and upper gully slopes. Collections by R. L. McGregor 10310, Greenwood County, 10199, Montgomery County; 10336, Elk County; W. H. Horr, July 5, 1930, Chautauqua County.

Allium canadense L., var. *lavendulare* (Bates) Ownby and H. C. Aase: Prairie pastures, roadsides, and open wooded slopes.

Allium stellatum Ker-Gawler: Sandy soil in scrub oak woods, open flood plain woods, roadsides, and prairie pastures.

Asparagus officinalis L.: Reported for Elk, Montgomery, and Woodson counties, Gates (1940).

Camassia scillioides (Raf.) Cory: Prairie hay fields, good grazed pastures, and open wooded slopes. Elk and Woodson counties.

Erythronium albidum Nutt.: Reported for Wilson County, Gates (1940).

Erythronium mesochoreum Knerr.: Low prairie woodlands and open scrub oak woods. Elk, Greenwood, and Woodson counties.

Hemerocallis fulva L.: Border of low woods. Found once, in Woodson County.

Nothoscordium bivalve (L.) Britton: In sandy soil of open oak woods and rocky prairie slopes. Chautauqua and Woodson counties.

Polygonatum canaliculatum (Muhl.) Pursh.: Along creek banks and in flood plain woods.

Smilax bona-nox L.: Thicket of flood plain woods. Collection by B. L. Wagenknecht 2228, Wilson County.

Smilax herbacea L.: Flood plain woods and in a prairie thicket of a prairie gulch. Elk and Woodson counties.

Smilax tamnoides L., var. *hispida* (Muhl.) Fern.: Creek banks and woodland borders. All counties except Elk and Woodson.

Yucca glauca Nutt., var. *mollis* Engelm.: Calcareous soil of prairie hillsides and hilltops. Collections by R. L. McGregor 4347, Montgomery County; 4309, Wilson County.

Zigadenus nuttallii Gray: Wooded gullies and prairie woodlands.

AMARYLLIDACEAE

Cooperia drummondii Herb.: Rocky prairie hillsides. Collections by W. H. Horr E232, Wilson County; W. C. Stevens 8177-1, Wilson County.

Hypoxis hirsuta (L.) Coville: Sandy soil of open scrub oak woods, and in prairie pastures.

IRIDACEAE

Belamcanda chinensis (L.) DC.: Escaped from cultivation and established in prairies and along roadsides. Collection by W. H. Horr, July 11, 1930, Woodson County.

Nemastylis geminiflora Nutt.: In prairie woodlands and pastures. Elk and Chautauqua counties.

Sisyrinchium campestre Bickn.: Prairie hay fields and pastures, along borders of creek woods, and in sandy soil of upland woods. Chautauqua and Woodson counties.

ORCHIDACEAE

Corallorhiza wisteriana Conrad.: On a wooded limestone escarpment. Found once by R. L. McGregor 10227, five miles northeast of Elk City, Montgomery County.

Hexalectris spicata (Walt.) Barhart: Growing through rich leaf mold of a wooded limestone escarpment. Collected once by R. L. McGregor 3393, five miles northeast of Elk City, Montgomery County.

Spiranthes cernua (L.) Richard: In sandy soil of open scrub oak woods. All counties except Elk and Wilson.

Spiranthes gracilis (Bigel) Beck: In low, grazed and ungrazed prairies. Collected once, in Woodson County.

Spiranthes vernalis Engelm. and Gray: Reported for Elk, Montgomery, and Wilson counties, Gates (1940).

SALICACEAE

Populus alba L.: Introduced and naturalized in wasteland woods and stream valleys. Montgomery and Wilson counties.

Populus deltoides Marsh: Gullies, streambanks, wasteland woods, and open flood plain woods.

Salix amygdaloides Anders.: Creek banks, wood gullies, and lowland woods. Chautauqua, Greenwood, and Woodson counties.

Salix caroliniana Michx.: Wooded gullies and stream banks. Chautauqua and Greenwood counties.

Salix eriocephala Michx.: Rocky prairie gullies. Rare. Woodson County.

Salix humilis Marsh., var. *microphylla* (Anders.) Fern.: Border of open oak woods. Rare. Montgomery County.

Salix humilis Marsh., var. *rigidiuscula* (Anders.) Rob.: Rocky open hillsides. Woodson County.

Salix interior Rowlee: Sandy stream banks. Collections by W. H. Horr 3378, Wilson County; B. L. Wagenknecht 1737; 1834, Chautauqua County.

Salix nigra Marsh., var. *nigra:* Wooded gullies and lowland woods.

Salix nigra Marsh., var. *lindheimeri* Schneider: Wooded gullies and flood plain woods. Collections by W. H. Horr, July 28, 1930, Greenwood County; P. A. Rydberg and R. Imler, Montgomery County.

JUGLANDACEAE

Carya cordiformis (Wang.) K. Koch., var. *cordiformis:* Creek banks, flood plain woods, and upland slopes.

Carya cordiformis (Wang.) K. Koch., var. *latifolia* Sarg.: Flood plain woods and stream banks. Collections by W. H. Horr, July 5, 1930, Chautauqua County; July 5, 1930, Montgomery County.

Carya illinoensis (Wang.) K. Koch: Open flood plain woods. Wilson and Woodson counties.

Carya laciniosa (Michx.) Loud.: Rich lowland woods. Collection by W. H. Horr, July 5, 1938, Chautauqua County.

Carya ovata (Mill.) K. Koch: Wooded gullies and flood plain woods.

Carya texana Buckl.: Reported for Montgomery and Wilson counties, Gates (1940).

Carya tomentosa (Poir.): Flood plain woods. Rare. Collection by W. H. Horr, July 5, 1930, Chautauqua County.

Juglans nigra L.: Low woodlands and upland wooded slopes.

BETULACEAE

Betula nigra L.: Base of a wooded slope above a creek. Found once, in Chautauqua County.

Corylus americana Walt.: Reported for Wilson County, Gates (1940).

Ostrya virginiana (Mill.) K. Koch: Flood plain woods and slopes of upland woods. Woodson County.

FAGACEAE

Quercus alba L.: Upland scrub oak woods. Found in one location, three miles southwest of Elk City, Montgomery County.

Quercus alba L. × *Q. muhlenbergii* Engelm.: On a wooded limestone escarpment. Rare. Collected five miles northeast of Elk City, Montgomery County.

× *Quercus bushii* Sarg.: Along sandstone escarpments, and slopes of upland woods.

× *Quercus faxoni* Trel.: Wooded limestone escarpments, slopes and borders of upland woods. Rare. Two locations in Montgomery County.

× *Quercus fernowi* Trel.: Sandstone escarpments, slopes and borders of open oak woods. Rare. Montgomery and Wilson counties.

Quercus imbricaria Michx.: Woods along a small creek. Found once by R. L. McGregor 4464, two miles north of Howard, Elk County.

Quercus macrocarpa Michx.: Flood plain woods, wooded upland gullies.
Quercus marilandica Muench.: Hilltops and slopes of upland woods. Frequent.
Quercus muehlenbergii Engelm.: Upland gullies, rocky escarpments, and slopes of upland woods.
Quercus muehlenbergii Engelm., forma *alexanderi* (Britt.) Trel.: Upland gullies, rocky escarpments, and slopes of upland woods.
Quercus palustris Muench.: Slopes of upland woods and creek valleys.
Quercus prinoides Willd.: Rocky escarpments, gullies, and slopes of upland woods.
Quercus rubra L.: In gullies and lower slopes of upland woods.
Quercus shumardii Buckl., var. *shumardii:* Slopes of upland woods. Rare. Collections from Greenwood and Montgomery counties.
Quercus shumardii Buckl., var. *schneckii* (Britton) Sarg.: Rocky escarpments, and slopes of upland woods.
Quercus stellata Wang.: Hilltops and slopes of upland woods. Frequent.
× *Quercus stelloides* E. J. Palmer: Upland wooded slopes, and limestone escarpments. Chautauqua, Montgomery, and Wilson counties.
Quercus velutina Lam.: Rocky escarpments, and slopes of upland woods.

ULMACEAE

Celtis laevigata Willd.: At the base of a scrub oak wooded hillside. Rare. Montgomery County.
Celtis occidentalis L.: Flood plain woods, and slopes and hilltops of upland woods.
Celtis reticulata Torr.: Reported for Wilson County, Gates (1940).
Celtis tenuifolia Nutt., var. *georgiana* (Small) Fern. and Schub.: Flood plain woods, rocky open slopes of uplands.
Ulmus americana L.: Flood plain woods, and slopes of uplands.
Ulmus rubra Muhl.: Low woodlands, wooded prairie gullies and upland slopes.

MORACEAE

Maclura pomifera (Raf.) Schneider: Wasteland woods and disturbed areas.
Morus alba L.: Flood plains and stream banks.
Morus rubra L.: Open flood plain woods and lower upland slopes.

CANNABINACEAE

Cannabis sativa L.: Reported for Chautauqua, Greenwood, and Montgomery counties, Gates (1940).
Humulus lupulus L.: Creek banks and flood plain woods. Collections by O. S. Fearing and G. Latham, August 10, 1950, Chautauqua County; W. H. Horr, July 5, 1930, Chautauqua and Montgomery counties; June 28, 1930, Greenwood County.

URTICACEAE

Boehmeria cylindrica (L.) S. W.: On wooded slopes, and rocky outcrops.
Laportea canadensis (L.) Wedd.: Moist low woods.
Parietaria pensylvanica Muhl.: Low woodlands and waste places.
Pilea pumila (L.) Gray, var. *deamii* (Lunell) Fern.: Moist soil of stream and creek banks. Woodson County.
Urtica procera Muhl.: Waste places. Woodson County.

LORANTHACEAE

Phoradendron flavescens (Pursh) Nutt.: Growing on *Ulmus americana* in a flood plain woods. Rare. Collected by R. L. McGregor 9860, Montgomery County.

Polygonum hydropiper L.: Flood plain woods and moist gulches in prairie pastures. Woodson County.

Polygonum hydropiperoides Michx.: Low woods and moist prairie gullies. Woodson County.

Polygonum hydropiperoides Michx., forma *strigosum* (Small) Stanford: Reported for Chautauqua County, Gates (1940).

Polygonum lapathifolium L.: Edges of pond and marshes. Woodson County.

Polygonum pensylvanicum L., var. *pensylvanicum*: Flood plain woods, prairie gullies, and waste places.

Polygonum pensylvanicum L., var. *laevigatum* Fern.: Waste places and flood plain woods. Woodson County.

Polygonum persicaria L.: Creek banks, borders of flood plain woods, and waste places.

Polygonum prolificum (Small) Robinson: Waste places and fields. Collection by W. H. Horr, July 5, 1930, Chautauqua County.

Polygonum punctatum Ell.: Creek banks, flood plain woods, temporary water holes in prairie gullies, and banks of ponds.

Polygonum ramosissimum Michx.: Waste places. Woodson County.

Polygonum scandens L.: Flood plain woods and thickets of upland slopes. Collections by W. H. Horr, June 28, 1930, Greenwood County; July 5, 1930, Chautauqua County; B. L. Wagenknecht 2224, Wilson County; 1697 Montgomery County.

Polygonum tenue Michx.: Prairie pastures and waste places. Woodson County.

Rumex acetosella L.: Roadsides, waste places, and borders of fields and woods. Woodson County.

Rumex alluvius Gates and McGregor: Flood plain woods, river banks. Collection by R. L. McGregor 5732, Wilson County.

Rumex altissimus Wood: Waste places, roadsides, and eroded prairie pastures.

Rumex crispus L.: Waste places and open flood plain woods. Collections by W. H. Horr, July 10, 1930, Woodson County; July 12, 1930, Wilson County; R. L. McGregor 3142, Woodson County.

Rumex hastatulus Baldw.: In sandy soil at borders of fields and waste places. Collection by W. H. Horr E259, Chautauqua County.

Rumex venosus Pursh.: Reported for Chautauqua and Greenwood counties, Gates (1940.)

Tovaria virginiana (L.) Raf.: Low open woodlands.

CHENOPODIACEAE

Chenopodium album L.: Waste places, fields, and overgrazed pastures.

Chenopodium ambrosiodes L.: Waste places and fields. Collection by W. H. Horr, July 11, 1930, Woodson County.

Chenopodium berlandieri Moq., subsp. *boscianum* (Moq.) Aellen: Low woodlands and waste places. Collections by B. L. Wagenknecht 1828, Chautauqua County; 2230, Wilson County.

Chenopodium botrys L.: In sandy soil of an exposed lake bed. Reported for Woodson County, McGregor and Volle (1950).

Chenopodium hybridum L., var. *gigantospermum* (Aellen) Rouleau.: Wooded prairie gully, and lowland creek woods.

Chenopodium pratericola Rydb.: Sandy soil of open woodlands. Collection by B. L. Wagenknecht 1698, Montgomery County.

Chenopodium subglabrum (S. Wats.) Nelson: Reported for Chautauqua County, Gates (1940).

Cycloloma atriplicifolium (Spreng.) Coult.: Dry exposed lake bed. Collection by R. L. McGregor 3188, Woodson County.

Monolepis nuttalliana (R. and S.) Greene: Rocky prairie hillside. Found once, in Woodson County.

Kochia scoparia (L.) Schrad.: Dry rocky prairie wasteland. Collection by R. L. McGregor 9780, Greenwood County.

AMARANTHACEAE

Amaranthus albus L.: Railroad embankments. Rare. Woodson County.

Amaranthus graecizans L.: Reported for Chautauqua, Greenwood, and Woodson counties, Gates (1940).

Amaranthus hybridus L.: Borders of fields and low woods, overgrazed pastures, and waste places.

Amaranthus retroflexus L.: In sandy soil of an exposed lake bed. Reported for Woodson County, McGregor and Volle (1950).

Amaranthus spinosus L.: Waste places and borders of fields. Collection by W. H. Horr, July 11, 1930, Woodson County.

Amaranthus tamariscinus Nutt.: Fields, waste places, pastures, and open grazed woodlands.

Froelichia floridana (Nutt.) Moq., var. *campestris* (Small) Fern.: Border of marsh in a prairie hay field. Woodson County.

Froelichia gracilis Moq.: Waste places, railroad embankments, and borders of fields. Wilson and Woodson counties.

Iresine rhizomotosa Standl.: Dry soil of fields and waste places. Collections by W. H. Horr E117, Montgomery County; R. H. Thompson, September 1, 1951, Woodson County.

NYCTAGINACEAE

Mirabilis albida (Walt.) Heimerl: In clay soil of a heavily grazed pasture. Collection by B. L. Wagenknecht 2249, Wilson County.

Mirabilis linearis (Pursh) Heimerl: In calcareous soil of a prairie pasture, and in rocky prairie gullies.

Mirabilis nyctaginea (Michx.) MacM.: Borders of low woods, roadsides, and railroad embankments. Greenwood and Woodson counties.

PHYTOLACCACEAE

Phytolacca americana L.: Open lowland woods and waste places.

AIZOACEAE

Glinus lotoides L.: On an alluvial deposit on an ox-bow of Fall River. Collection by R. L. McGregor 5730, Wilson County.

Mollugo verticillata L.: Low prairie woodlands. Chautauqua and Woodson counties.

PORTULACACEAE

Claytonia virginica L.: In sandy soil of prairie pastures and open upland woods.

Portulaca oleracea L.: In sandy soil of open upland woods. Collections by W. H. Horr, July 28, 1930, Greenwood County; R. L. McGregor 3171, Woodson County.

Portulaca parvula Gray: In sandy soil of open scrub oak woods, and in rocky wooded gullies. Wilson and Woodson counties.

Talinum calycinum Engelm.: Reported for Wilson County, Gates (1940).

Talinum parviflorum Nutt.: In shallow soil over sandstone outcrops in scrub oak woods. Chautauqua and Woodson counties.

CARYOPHYLACEAE

Agrostemma githago L.: Borders of fields, waste places. Collection by W. H. Horr E163, Woodson County.

Arenaria patula Michx.: In rocky prairie pastures, and open upland woods. Woodson County.

Arenaria stricta Michx., var. *texana* Robins.: Rocky slopes of upland woods. Collection by R. L. McGregor 10196, Montgomery County.

Cerastium brachypodium (Engelm.) Robinson: Prairie pasture hillsides, roadside ditches, and borders of fields.

Cerastium bulgatum L.: Reported for Montgomery County, Gates (1940).

Sagina decumbens (Ell.) T. and G.: Reported for Chautauqua County, Gates (1940).

Saponaria officinalis L.: Roadsides and waste places. Woodson County.

Silene antirrhina L.: In flood plain woods, wooded gullies in prairie pastures. Wilson and Woodson counties.

Silene stellata (L.) Ait. f., var. *scabrella* (Niewl) Palmer and Steyermark: In dense flood plain woods and wooded gullies.

Stellaria media (L.) Cyrillo: Roadsides, waste places, and borders of fields.

ILLECEBRACEAE

Paronychia canadensis (L.) Wood: In moist shallow soil over limestone outcrops of a prairie pasture hillside. Found once, in Woodson County.

Paronychia fastigiata (Raf.) Fern.: In sandy soil of open oak woods. Montgomery and Woodson counties.

NYMPHAEACEAE

Nelumbo lutea (Willd.) Pers.: In water along the shore of a woodland marsh. Montgomery County.

RANUNCULACEAE

Anemone caroliniana Walt.: In prairie pastures and prairie woodlands.

Anemone caroliniana Walt., forma *violacea* Clute: In prairie pastures and prairie woodlands.

Aquilegia canadensis L., var. *latiuscula* (Greene) Munz.: In crevices of limestone and sandstone outcrops in upland woods. Rare. Chautauqua, Greenwood, and Montgomery counties.

Clematis pitcheri T. and G.: In dense flood plain woods, and thickets.

Delphinium ajacis L.: Escaped from cultivation and established along roadsides and waste places.

Delphinium tricorne Michx.: In dense undergrowth of flood plain woods. Chautauqua and Woodson counties.

Delphinium virescens Nutt., var. *virescens:* Prairie hay fields, open creek valley woods, and roadsides.

Delphinium virescens Nutt., var. *penardi* (Huth) Perry: Reported for Chautauqua and Woodson counties, Gates (1940).

Isophyrum biternatum (Raf.) T. and G.: Open wooded hillside. Collection by R. L. McGregor 9012, Greenwood County.

Myosurus minimus L.: Bank of a prairie pasture pond. Woodson County.

Ranunculus abortivus L.: Banks of runoff streams in prairie pastures and open woods. Woodson County.

Ranunculus facicularis Muhl., var. *fascicularis*: Sandy soil of open scrub oak woods. Woodson County.

Ranunculus fascicularis Muhl., var. *apricus* (Greene) Fern.: Oak-hickory wooded hillside. Collection by R. L. McGregor 4815, Woodson County.

Ranunculus sceleratus L.: Temporary moist depressions in prairie woodlands. Woodson County.

Thalictrum dasycarpum Fisch. and Lall., var. *dasycarpum*: In dense undergrowth of flood plain woods. Woodson County.

Thalictrum dasycarpum Fisch. and Lall., var. *hypoglaucum* (Rydb.) Boivin: Reported for Greenwood, Wilson, and Woodson counties, Gates (1940).

ANNONACEAE

Asimina triloba Dunal: In dense flood plain woods.

MENISPERMACEAE

Cocculus carolinus (L.) DC.: In rocky open woods. Collection by W. H. Horr, July 5, 1930, Chautauqua and Montgomery counites.

Menispermum canadensis L.: In low woodlands. Wilson and Woodson counties.

BERBERIDACEAE

Podophyllum peltatum L.: Oak-hickory wooded slopes. Woodson County.

PAPAVERACEAE

Argemone polyanthemos (Tedde) Ownbey: Reported for Elk County, Gates (1940.)

Papaver rhoeas L.: In sandy soil along a stream in a prairie pasture. Found once, in Chautauqua County.

FUMMARIACEAE

Corydalis aurea Willd., var. *occidentalis* Engelm.: Reported for Chautauqua County, Gates (1940).

Corydalis crystallina Engelm.: In shallow soil over sandstone outcrops in open oak woods, and roadside banks.

Corydalis micrantha (Engelm.) Gray: Fields and roadside banks. Elk and Woodson counties.

Dicentra cucullaria (L.) Bernh.: Wooded creek bank. Collections by R. L. McGregor 10343, Elk County; B. L. Wagenknecht 1855a, Chautauqua County.

CRUCIFERAE

Alliaria officinalis Andrz.: In low creek woodlands. Elk County.

Arabis canadensis L.: In shallow soil over limestone outcrops in a wooded ravine, and on a limestone wooded escarpment. Collections by R. L. McGregor 10372, Elk County; 10224, Montgomery County.

Brassica juncea (L.) Coss.: Reported for Elk County, Gates (1940).

Brassica nigra (L.) Koch: Reported for Greenwood and Wilson counties, Gates (1940).

Brassica rapa L.: In open woods bordering cultivated field. Elk County.

Camelina microcarpa Andrz.: Disturbed prairie pastures. Montgomery and Woodson counties.

Camelina sativa (L.) Crantz.: Sandy soil of roadside bank covered by bluestem. Collection by R. L. McGregor 10195, Montgomery County.

Capsella bursa-pastoris (L.) Medic.: Waste places, and overgrazed pastures.

Cardamine parviflora L., var. *arenicola* (Britt.) O. E. Schulz. Dry exposed bed of a lake. Collection by R. L. McGregor 3165, Woodson County.

Dentaria laciniata Muhl.: Wooded hillside along a small creek, and on a wooded creek bank. Collections by R. L. McGregor 9056, Elk County; 9015, Greenwood County.

Descurainia pinnata (Walt.) Britt., subsp. *pinnata*: Sandy soil of prairie pastures, and roadsides

Descurainia pinnata (Walt.) Britt., subsp. *brachycarpa* (Richard) Detling.: Edge of a rocky disturbed prairie pasture. Collection by R. L. McGregor 4333, Montgomery County.

Descurainia pinnata (Walt.) Britt., subsp. *intermedia* (Rydb.) Detling: Reported for Wilson County, Gates (1940.)

Descurainia sophia (L.) Webb: Reported for Chautauqua County, Gates (1940).

Draba brachycarpa Nutt.: In rocky prairie pastures, open upland woods, and roadsides.

Draba cuneifolia Nutt.: Shallow soil over surfacing sandstone and limestone in prairie pastures, and open upland woods. Collections by R. L. McGregor 9047, Chautauqua County; 9053, Elk County; 9035, Montgomery County; 9033, Wilson County; 9005, Woodson County.

Draba reptans (Lam.) Fern., var. *reptans*: In sandy soil of prairie pastures, and open upland woods.

Draba reptans (Lam.) Fern., var. *micrantha* (Nutt.) Fern.: Reported for Greenwood County, Gates (1940).

Erysimum repandum L.: On sandy soil of open scrub oak woods, and waste places.

Iodanthus pinnatifidus (Michx.) Steud.: On wooded creek banks. Woodson County.

Lepidium densiflorum Schrad.: Prairie pastures, roadsides, and waste places.

Lepidium virginicum L.: Borders of low woods, fields, and waste places.

Lesquerella gracilis (Hook) S. Wats., var. *repanda* (Nutt.) Payson: Sandy rocky soil of pastures, roadsides, and fields. Woodson County.

Nasturtium officinale R. Br.: Prairie pastures swale just below a spring. Collection by R. L. McGregor 10257, Wilson County.

Rorippa islandica (Oeder ex Muir) Borbas, var. *hispida* (Desv.) Butt. and Abbe: Dry exposed lake bed. Collection by R. L. McGregor 3161, Woodson County.

Rorippa obtusa (Nutt.) Britt.: Border of lowland field. Collection by W. H. Horr, July 11, 1930, Woodson County.

Rorippa sessiliflora (Nutt.) Hitchc.: Creek banks, flood plain woods, and in sandy soil of an exposed lake bed. Woodson County.

Rorippa sinuata (Nutt.) Hitchc.: Low wooded creek valleys, and waste places. Woodson County.

Selenia aurea Nutt.: Sandy soil of open upland woods. Montgomery and Woodson counties.

Sibara virginica (L.) Rollins: Open prairie woodlands.

Sisymbrium officinale (L.) Scop., var. *officinale*: In low prairie pastures, roadsides, and borders of fields. Wilson and Woodson counties.

Sisymbrium officinale (L.) Scop., var. *leiocarpum* DC.: Reported for Greenwood County, Gates (1940).

Thlaspi arvense L.: Prairie pastures, roadsides, and waste places.

Crassulaceae

Sedum nuttalianum Raf.: In shallow soil over surfacing sandstone in prairie pastures. Chautauqua and Montgomery counties.

Sedum pulchellum Michx.: In shallow soil over surfacing limestone and sandstone of prairie pastures. Montgomery and Wilson counties.

Saxifragaceae

Heuchera richardsonii R. Br., var. *grayana* Rosend., Butt. and Lak.: In crevices of sandstone outcrops of oak wooded slopes. Chautauqua, Greenwood, and Woodson counties.

Penthorum sedoides L.: In sandy soil of an exposed lake bed, and in an open oak woods. Collection by W. H. Horr 232-1, Wilson County; reported for Woodson County, McGregor and Volle (1950).

Ribes missouriense Nutt.: Low woodland slopes, and wooded gullies in uplands.

Ribes odoratum Wendland f.: Reported for Greenwood County, Gates (1940).

Saxifraga texana Buckl.: In sandy soil of a high prairie woodland. Rare. Collections by R. L. McGregor 9050, 4176, 1208, Chautauqua County.

Platanaceae

Platanus occidentalis L.: Low woodlands, and ravines of upland woods.

Rosaceae

Agrimonia gryposepala Wallr.: Reported for Elk County, Gates (1940).

Agrimonia parviflora Ait.: Reported for Woodson County, Gates (1940).

Agrimonia pubescens Wallr.: In shallow soil over a sandstone outcrop of an oak-hickory wooded hillside. Woodson County.

Amelanchier arborea (Michx.) Fern.: Rocky wooded hillsides. Elk and Chautauqua counties.

Crataegus crus-galli L.: Rocky prairie woodland hillsides, and along border of upland woods. Collections by R. L. McGregor 10258, Wilson County; B. L. Wagenknecht 2195, Wilson County.

Crataegus mollis (T. and G.) Scheele: Upland wooded gullies. Chautauqua County.

Crataegus stevensiana Sarg.: Reported for Montgomery County, Gates (1940).

Crataegus succulenta Link, var. *pertomentosa* (Ashe) Palmer: Reported for Montgomery County, Gates (1940).

Crataegus viridis L.: Lower slopes of oak wooded hillsides. Montgomery County.

Fragaria virginiana Duchesne, var. *virginiana*: In sandy soil of open wooded slopes. Chautauqua County.

Fragaria virginiana Duchesne, var. *illinoensis* (Prince) Gray: Reported for Elk, Montgomery, and Wilson counties, Gates (1940).

Fragaria vesca L., var. *americana* Porter: Sandy soil of open upland woods. Collections by W. H. Horr, July 5, 1930, Montgomery County; June 28, 1930, Greenwood County.

Geum canadense Jacq., var. *canadense*: Stream banks, and flood plain woods.

Geum canadense Jacq., var. *camporum* (Rydb.) Fern. and Weath.: Flood plain woods, and in wooded prairie pasture gullies.

Geum vernum (Raf.) T. and G.: Reported for Montgomery County, Gates (1940).

Potentilla arguta Pursh.: Wooded creek banks. Chautauqua County.

Potentilla paradoxa Nutt.: Border of a rocky prairie pasture, and on a wooded limestone escarpment. Rare. Chautauqua County.

Potentilla simplex Michx.: Open wooded hillsides, and prairie pasture gullies. Chautauqua and Woodson counties.

Prunus americana Marsh., var. *americana*: Flood plain woods, and upland wooded gullies.

Prunus americana Marsh., var. *lanata* Sudw.: Reported for Elk County, Gates (1940).

Prunus angustifolia Marsh., var. *angustifolia*: Low woodlands. *Prunus angustifolia* Marsh., var. *watsonii* (Sarg.) Waugh.: Creek valley wood-lands.

Prunus hortulana Bailey: Reported for Montgomery and Wilson counties, Gates (1940).

Prunus mexicana S. Wats.: Reported for Chautauqua, Montgomery, and Wilson counties, Gates (1940).

Prunus munsoniana Wight and Hedrick: Reported for Chautauqua and Elk counties, Gates (1940).

Prunus serotina Ehrh.: Low woodlands, and upland wooded slopes.

Prunus virginiana L.: Flood plain woods, and wooded upland gullies.

Rosa arkansana Porter, var. *suffulta* (Greene) Cockerell: Low prairie woodlands, thickets, and prairie pasture gulches.

Rosa blanda Ait.: Reported for Chautauqua, Montgomery, and Wilson counties, Gates (1940).

Rosa rubifolia R. Br.: Reported for Chautauqua, Montgomery, and Wilson counties, Gates (1940).

Rosa setigera Michx.: Prairie thickets, and low open woods. Woodson County.

Rubus allegheniensis Porter: Prairie pastures, roadsides, and woodland thickets.

Rubus ostryifolius Rydb.: Reported for Woodson County, Gates (1940).

Rubus flagellaris Willd.: Open wooded hillsides, and prairie woodlands.

Rubus occidentalis L.: Prairie thickets, roadsides, and open wooded slopes.

Leguminosae

Acacia angustissima (Mill) Ktze., var. *hirta* (Nutt.) Robinson: Reported for Chautauqua and Montgomery counties, Gates (1940).

Amorpha canescens Pursh.: Prairie hay fields, pastures, and prairie woodlands.

Amorpha fruticosa L., var. *fruticosa*: Prairie hay fields, pastures, and open upland woods.

Amorpha fruticosa L., var. *angustifolia* Pursh.: Grazed and ungrazed prairies, and prairie woodlands.

Amphicarpa bracteata (L.) Fern., var. *bracteata*: Thickets of low woodlands. Collection by B. L. Wagenknecht 1718, Montgomery County.

Amphicarpa bracteata (L.) Fern., var. *comosa* (L.) Fern.: Reported for all counties except Greenwood and Wilson, Gates (1940).

Apios americana Medic., var. *turrigera* Fern.: Reported for all counties except Greenwood and Wilson, Gates (1940.)

Astragalus canadensis L.: Creek valley grassland. Collection by W. H. Horr and R. L. McGregor E212, Woodson County.

Astragalus caryocarpus Ker.: Rocky prairie hay fields and pastures.

Astragalus lotiflorus Hook.: Reported for Woodson County, Gates (1940.)

Baptisia leucantha T. and G.: Prairie hay fields, good grazed pastures, and prairie woodlands.

Baptisia leucophaea Nutt.: Grazed and ungrazed prairies, and prairie woodlands.

Baptisia minor Lehm.: Prairie hay fields, pastures, and prairie woodlands.

Cassia fasciculata Michx.: Prairie hay fields, pastures, roadsides, and open wooded slopes.

Cassia marilandica L.: Rocky prairie gully. Collection by R. L. McGregor 10864, Wilson County.

Cassia nictitans L.: In undergrowth of open upland wooded hillside. Collection by R. L. McGregor 4087, Woodson County.

Cercis canadensis L.: Creek valleys and open wooded slopes.

Cercis canadensis L., forma *glabrifolia* Fern.: Thicket along a creek bank. Rare. Collection by R. L. McGregor 4461, Woodson County.

Crotalaria sagittalis L.: Creek banks, and open woodlands. Montgomery and Woodson counties.

Dalea candida Willd.: Low prairie hay fields and pastures.

Dalea laxiflora Pursh: Prairie hay fields and pastures. Collection by O. S. Fearing and G. Latham, August 14, 1950, Wilson County.

Dalea multiflora (Nutt.) Shinners: Prairie woodlands. Chautauqua and Woodson counties.

Dalea purpurea Vent: Grazed and ungrazed prairies, and prairie woodlands.

Desmanthus illinoensis (Michx.) MacM.: Prairie thickets, roadsides, and open woods.

Desmodium canadense (L.) DC.: Reported for Chautauqua and Montgomery counties, Gates (1940).

Desmodium canescens (L.) DC.: Lowland wooded slope. Collection by B. L. Wagenknecht 1819, Chautauqua County.

Desmodium cuspidatum (Muhl. ex Willd.) Loud., var. *longifolium* (T. and G.) Schub.: Reported for Chautauqua County, Gates (1940).

Desmodium glutinosum (Muhl. ex Willd.) Wood: Gully banks, and wooded hillsides. Montgomery and Woodson counties.

Desmodium illinoensis Gray: Low woodlands and upland wooded hillsides.

Desmodium marilandicum (L.) DC.: Open scrub oak woods. Woodson County.

Desmodium nudiflorum (L.) DC.: Rocky open woods. Collection by B. L. Wagenknecht 1685, Montgomery County.

Desmodium paniculatum (L.) DC.: Wooded gullies, and open oak woods. Woodson County.

Desmodium pauciflorum (Nutt.) DC.: Dense upland woods. Collection by B. L. Wagenknecht 2245, Wilson County.

Desmodium perplexum Schub.: Reported for Montgomery and Woodson counties, Gates (1940.)

Desmodium sessilifolium (Torr.) T. and G.: Lower slopes of upland woods. Montgomery and Woodson counties.

Gleditsia triacanthos L.: Creek valley woodlands, and prairie thickets.

Glycyrrhiza lepidota (Nutt.) Pursh: Low prairies, and waste places. Collection by W. H. Horr, July 5, 1930, Montgomery County.

Gymnocladus dioica (L.) Koch: Flood plain woods, and slopes of upland woods.

Lespedeza capitata Michx.: Low prairie hay field. Collection by W. H. Horr, July 11, 1930, Woodson County.

Lespedeza repens (L.) Bart.: Reported for Elk and Woodson counties, Gates (1940).

Lespedeza striata (Thunb.) H. and A.: Dry exposed lake bed. Collection by R. L. McGregor 4106, Woodson County.

Lespedeza stuvei Nutt.: Slopes of open upland woods. Woodson County.

Lespedeza violacea (L.) Pers.: Prairie hay fields, and rocky prairie hillsides.

Lespedeza virginica (L.) Britt.: Open wooded hillsides.

Medicago lupulina L.: Roadsides, fields, and waste places.

Medicago sativa L.: Roadsides, fields, and waste places.

Melilotus alba Desf.: Low prairies, roadsides, and waste places.

Melilotus officinalis (L.) Lam.: Low prairies, roadsides, and waste places.

Psoralea argophylla Pursh: Slopes and crests of rocky prairie pastures. Collections by W. H. Horr, July 28, 1930, Greenwood County; R. L. McGregor 10347, Elk County.

Psoralea esculenta Pursh: Prairie pastures. Woodson County.

Psoralea tenuiflora Pursh: Prairie hay fields, pastures, and prairie woodlands.

Robinia pseudo-acacia L.: Open flood plain woods, pasture gullies, and prairie thickets.

Schrankia uncinata Willd.: Prairie thickets, roadsides, and rocky pasture hillsides.

Sesbania exalata (Raf.) Cory: In alluvial soil of an ox bow of Fall River. Collections by R. L. McGregor 5728, Montgomery County; 5729, Wilson County.

Sophora sericea Nutt.: Reported for Woodson County, Gates (1940).

Strophostyles helvola (L.) Britton: Sandy soil of open upland woods. Montgomery and Woodson counties.

Strophostyles leiosperma (T. and G.) Piper: Sandy soil of open scrub oak woods. Woodson County.

Stylosanthes biflora (L.) BSP., var. *biflora*: Prairie hay fields, pastures, and prairie woodlands.

Stylosanthes biflora (L.) BSP., var. *hispidissima* (Michx.) Pollard and Ball: Prairie hay field and pastures. Woodson County.

Tephrosia leucosericea (Rydb.) Cory: Reported for Elk and Chautauqua counties, Gates (1940).

Tephrosia virginiana (L.) Pers.: Prairie hay fields, pastures, and prairie woodlands.

Trifolium campestre Schreb.: Rocky prairie pasture hillsides. Collections by R. L. McGregor 4320, Montgomery County; 4286, Wilson County.

Trifolium pratense L.: Fields, roadsides, and waste places.

Trifolium repens L.: Fields, roadsides, and waste places.

Vicia villosa Roth.

Linaceae

Linum sulcatum Riddell: Low prairie hay fields and pastures.

Linum usitatissimum L.: Reported for Greenwood County, Gates (1940).

Oxalidaceae

Oxalis corniculata L.: Creek valley woods. Collection by W. H. Horr, July 28, 1930, Greenwood County.

Oxalis europaea Jord., var. *europaea*: Prairies and rocky woodlands.

Oxalis europea Jord., var. *europaea*, forma *pilosella* Wieg.: Rocky prairie hillside bordering an oak woods. One collection from Chautauqua County.

Oxalis europaea Jord., var. *bushii* (Small) Wieg.: Prairies and open woods. Collections by W. H. Horr, June 28, 1930, Greenwood County; July 5, 1930, Montgomery County; R. L. McGregor 3168, Woodson County.

Oxalis stricta L.: Rocky pastures, roadsides, and open woodlands.

Oxalis violacea L.: Prairie hay fields, pastures and roadsides.

Oxalis violacea L., forma *albida* Fassett.: In a low prairie hay field. Found once, in Chautauqua County.

Geraniaceae

Geranium carolinianum L.: Prairies, roadsides, and open wooded hillsides.

Rutaceae

Ptelea trifoliata L.: Borders of flood plain woods, and upland wooded hillsides.

Zanthoxylum americanum Mill.: Open woodlands, and in shallow soil of a wooded limestone escarpment. Elk, Chautauqua, and Greenwood counties.

Zygophyllaceae

Tribulus terrestria L.: Roadsides and waste places.

Simarubaceae

Ailanthus altissima Swingle: Low open woodland. Collections by W. H. Horr, July 5, 1930, Chautauqua and Montgomery counties.

Polygalaceae

Polygala incarnata L.: Prairies and open woodlands. Woodson County.

Polygala sanguinea L.: Prairies and open oak woods.

Polygala sanguinea L., forma *albiflora* (Wheelock) Millsp.: Prairie pastures. Rare. Montgomery and Woodson counties.

Polygala sanguinea L., forma *viridescens* (L.) Farw.: Prairies and grassy banks in open creek woods. Collections by W. H. Horr, July 11, 1930, Woodson County; P. A. Rydberg 431, Montgomery County.

Polygala verticillata L., var. *isocycla* Fern.: Prairie pasture. Collection by P. A. Rydberg and R. Imler 457, Montgomery County.

EUPHORBIACEAE

Acalypha gracilens Gray, var. *gracilens:* In sandy soil of open upland woods.

Acalypha gracilens Gray, var. *fraseri* (Muell, Arg.) Weath.: In shallow soil over sandstone outcrops of a moist gully in a prairie woodland. Collection by R. L. McGregor 10804, Chautauqua County.

Acalypha gracilens Gray, var. *monococca* Engelm.: In shallow soil under a limestone ledge of a wooded hillside, and in sandy soil of an open oak woods. Collections by R. L. McGregor 10823, Chautauqua County; 10842, Montgomery County.

Acalypha rhomboidea Raf.: Roadsides, and border of a low woodland. Woodson County.

Acalypha virginica L.: Roadsides, and open flood plain woods.

Croton capitatus Michx.: Roadsides, overgrazed pastures, and waste places.

Croton glandulosus L., var. *septentrionalis* Muell Arg.: Roadsides and waste places. Collections by W. H. Horr, July 5, 1930, Chautauqua and Montgomery counties.

Croton monanthogynus Michx.: Overgrazed pastures, roadsides, and open lowland woods.

Croton texensis (Klotzch) Muell. arg.: Reported for Montgomery County, Gates (1940).

Crotonopsis elliptica Willd.: In sandy soil of open upland woods. Collection by R. L. McGregor 10817, Chautauqua County.

Ditaxis mercurialina (Nutt.) Coult.: Rocky prairie hay fields and pastures. Collections by R. L. McGregor 4342, Montgomery County; 4923, Wilson County.

Euphorbia corollata L.: Low prairie hay fields, pastures, and prairie woodlands.

Euphorbia dentata Michx.: Open woodlands and waste places.

Euphorbia dictyosperma Fisch. and Mey.: Roadsides, waste places, and open flood plain woods.

Euphorbia heterophylla L.: Sandy soil of open oak woods, borders of flood plain woods, fields, and roadsides.

Euphorbia hexagona Nutt.: Sandy soil of low open woods, and fields. Collection by B. L. Wagenknecht 1684, Montgomery County.

Euphorbia humistrata Engelm.: Rocky prairie pasture. Collection by B. L. Wagenknecht 2183, Wilson County.

Euphorbia maculata L.: Overgrazed pastures, rocky open wooded gullies, roadsides, and waste places.

Euphorbia marginata Pursh.: In prairie gullies, roadsides, and waste places. Chautauqua and Woodson counties.

Euphorbia missurica Raf., var. *missurica:* In an overgrazed pasture, and in rocky waste places. Collections by W. H. Horr, July 11, 1930, Woodson County; B. L. Wagenknecht 1679, Montgomery County.

Euphorbia missurica Raf., var. *intermedia* (Engelm.) L. C. Wheeler: Shallow soil over limestone surfacing in prairie pasture. Collection by B. L. Wagenknecht 1860, Chautauqua County.

Euphorbia obtusata Pursh.: Overgrazed pastures, rocky prairie gullies, and wooded hillsides.

Euphorbia serpens HBK.: Roadsides, fields, and waste places. Chautauqua and Woodson counties.

Stillingia sylvatica L.: Flood plain woods. Collections by P. A. Rydberg and R. Imler 394, Montgomery County.

Tragia urticifolia Michx.: Rocky pastures and moist ravine banks in upland woods. Collections by W. H. Horr, July 5, 1930, Chautauqua County; R. L. McGregor 10367, Elk County; 10829, Chautauqua County; B. L. Wagenknecht 1849, Chautauqua County.

CALLITRICHACEAE

Callitriche heterophylla Pursh.: In sandy soil of a dry exposed lake bed. Collection by R. L. McGregor 3179, Woodson County.

ANACARDIACEAE

Rhus aromatica Ait., var. *aromatica:* Rocky prairie pastures, and wooded upland slopes. Collection by B. L. Wagenknecht 1868, Chautauqua County.

Rhus aromatica Ait., var. *serotina* (Greene) Rehd.: Rocky prairie gullies, and prairie woodlands.

Rhus copallina L.: Prairie thickets, low rocky woods, and open upland wooded slopes.

Rhus glabra L.: Prairie thickets, low rocky woodlands, and open oak wooded hillsides.

Rhus radicans L., var. *rydbergii* (Small) Rehd.: Wooded upland gully, creek banks, and low woodlands. Woodson County.

Rhus radicans L., var. *vulgaris* (Michx.) DC. forma *negundo* (Greene) Fern.: Wooded gullies, and flood plain woods. Frequent.

AQUIFOLIACEAE

Ilex decidua Walt.: Reported for Montgomery County, Gates (1940).

CELASTRACEAE

Celastrus scandens L.: Thickets, wooded cliff, and dense low woods.

Euonymus atropurpureus Jacq.: Wooded stream banks, creek valleys, and wooded hillsides. Elk and Woodson counties.

STAPHYLEACEAE

Staphylea trifolia L.: Creek banks, flood plain woods, and upland wooded slopes. Chautauqua and Greenwood counties.

ACERACEAE

Acer negundo L.: Stream banks, flood plain woods, and prairie thickets.

Acer saccharinum L.: Flood plain woods, and lower slopes of upland woods.

HIPPOCASTANACEAE

Aesculus glabra Willd., var. *glabra:* Creek bank thicket. Collection by W. H. Horr, July 11, 1930, Woodson County.

Aesculus glabra Willd., var. *sargentii* Rehd.: Creek banks, flood plain woods, lower slopes of rocky wooded hillsides, and wooded gullies. Chautauqua, Wilson and Woodson counties.

SAPINDACEAE

Sapindus drummondi H. and A.: On a wooded limestone plateau, and in a low woodland. Chautauqua and Montgomery counties.

BALSAMINACEAE

Impatiens pallida Nutt.: Low dense woodlands. Woodson County.

RHAMNACEAE

Ceanothus americana L., var. *pitcheri* T. and G.: Banks of streams and lakes, low woods, and gullies in uplands.

Ceanothus herbaceus Raf., var. *herbaceus:* Bank of moist prairie gully. Chautauqua County.

Ceanothus herbaceus Raf., var. *pubescens* (T. and G.) Shinners: Wooded creek bank bordering upland woods. Collection by W. H. Horr, June 28, 1930, Greenwood County.

Rhamnus lanceolata Pursh.: Reported for Wilson County, Gates (1940).

VITACEAE

Ampelopsis cordata Michx.: Growing over small trees and shrubs in a low woods, thickets in flood plain woods, and wooded gullies. All counties except Chautauqua and Elk.

Parthenocissus inserta (Kerner) K. Fritsch: Reported for Wilson County, Gates (1940).

Parthenocissus quinquefolia (L.) Planch.: Dense undergrowth of low woods, and slopes of upland woods. All counties except Elk and Wilson.

Vitis cinera Engelm: Growing over and hanging from branches of trees and flood plain woods.

Vitis vulpina L.: Growing among trees of flood plain woods. Collections by W. H. Horr, July 11, 1930, Woodson County; E198, July 5, 1930, Montgomery County; P. A. Rydberg, and R. Imler 386, Montgomery County.

MALVACEAE

Abutilon theophrasti Medic.: Low overgrazed prairie pasture, in sandy soil of an exposed lake bed, and waste places. Collections by W. H. Horr, June 28, 1930, Greenwood County; July 11, 1930, Woodson County; B. L. Wagenknecht 1804, Chautauqua County. Reported for Woodson County by McGregor and Volle (1950).

Callirhoe alcaeoides (Michx.) Gray: Rocky open wooded banks in creek valleys, and prairie woodlands.

Callirhoe involucrata (T. and G.) Gray: Rocky prairie hillsides, and low prairie woodlands. Chautauqua and Woodson counties.

Callirhoe leiocarpa Martin: Prairie hillside. Collection by R. L. McGregor 10358, Elk County.

Hibiscus militaris Cav.: In alluvial soil along Fall River, flood plain swamp, and on a dam of a small lake. Montgomery, Wilson, and Woodson counties.

Hibiscus trionum L.: In sandy soil of an exposed lake bed, roadsides, prairies, and waste places.

Malva neglecta Wallr.: Along the edge of a cultivated field. Collected once, in Woodson County.

Sida spinosa L.: Rocky prairie gully, open wooded park bordering Neosho River, and waste places. Chautauqua, Wilson, and Woodson counties.

Sidopsis hispida (Pursh) Rydb., emend Kearney: Reported for Wilson County, Gates (1940).

GUTTIFERAE

Hypericum drummondii (Greb. and Hook.) T. and G.: Prairie pasture gullies, and rocky slopes of upland woods. Chautauqua, Montgomery, and Woodson counties.

Hypericum mutilum L.: In sandy soil of a dry exposed lake bed, in shallow soil over sandstone outcrops of stream banks, and on steep slopes of wooded uplands. Montgomery and Woodson counties.

Hypericum perforatum L.: Reported for Woodson County, Gates (1940).

Hypericum punctatum Lam.: Roadside thickets, creek valley, and in rocky prairie pasture gullies. Chautauqua and Montgomery counties.

Hypericum spaerocarpum Michx.: Rocky prairie gullies, rocky wooded hillsides, and roadsides.

CISTACEAE

Helianthemum bicknellii Fern.: Rocky wooded gullies, prairie pasture gulches, and rocky wooded hillsides. Montgomery and Woodson counties.

Lechea tenuifolia Michx.: Creek valley thicket, sandy soil over surfacing sandstone of upland wooded slopes, and rocky banks in creek woods. All counties except Elk and Greenwood.

VIOLACEAE

Hybanthus linearis (Torr.) Shimers: Low prairies, banks of prairie gullies, and open woodlands. Elk, Wilson, and Montgomery counties.

Viola kitaibeliana Roem. and Schultz, var. *rafinesquii* (Greene) Fern.: Prairie hay fields, pastures, prairie woodlands, and roadsides.

Viola papilionacea Pursh: Open flood plain woods, and prairie woodlands. Chautauqua and Woodson counties.

Viola pedata L., var. *linearíloba* DC.: In sandy soil of open oak woods, and in shallow soil over surfacing sandstone of prairie pasture slopes. Chautauqua and Woodson counties.

Viola pedatifida G. Don: Rocky sandy soil of a prairie pasture hillside. Collection by R. L. McGregor 4801, Woodson County.

Viola pennsylvanica Michx.: Lowland wood, and low prairie woodlands. Woodson County.

Viola sororia Willd.: Along the border of a low woods. Collection by R. L. McGregor 4179, Chautauqua County.

PASSIFLORÀCEAE

Passiflora incarnata L.: In an open flood plain woods. Collections by W. H. Horr, July 11, 1930, E426, Montgomery County.

Passiflora lutea L., var. *glabriflora* Fern.: Lowland woods, and slopes of upland woods. Collections by W. H. Horr, July 21, 1942, E460, Montgomery County.

LOASACEAE

Mentzelia oligosperma Nutt.: Sandy soil of open wooded hillsides, prairie hilltops, and waste places. All counties except Greenwood and Wilson.

CACTACEAE

Mamillaria similis Engelm.: Rocky low pastures, and rocky slopes of prairie woodlands. Montgomery County.

Opuntia humifusa Raf.: Rocky overgrazed pastures. Collections by W. H. Horr, July 5, 1930, Chautauqua County; July 11, 1930, Woodson County.

Opuntia macrorhiza Engelm.: Rocky gullies, and prairie pastures.

LYTHRACEAE

Ammannia coccinea Rottb.: Border of a marsh in a low woods, in sandy soil of open oak woods, and on an exposed lake bed. Wilson and Woodson counties.

Lythrum californicum T. and G.: Hilltops and slopes of prairie pastures, and prairie woodlands.

Rotala ramosior (L.) Koekne, var. *interior* Fern. and Grisc.: Wet roadside ditch. Collection by W. H. Horr E157, Wilson County.

ONAGRACEAE

Circaea quadrisulcata (Maxim.) French. and Sav., var. *canadensis* (L.) Hara: Reported for Greenwood County, Gates (1940).

Gaura biennis L., var. *pitcheri* Pickering: Rocky prairie slopes, and low prairie woodlands. Woodson County.

Gaura coccinea Nutt.: Rocky prairie hillsides, and in a low woodland. Woodson County.

Gaura parviflora Dougl.: Rocky overgrazed prairie pasture slopes. All counties except Elk and Wilson.

Jussiaea repens L., var. *glabrescens* Ktze.: In shallow water of streams and woodland ravines. Wilson and Woodson counties.

Ludwigia alternifolia L., var. *alternifolia:* Rocky banks of prairie pastures. Woodson County.

Ludwigia alternifolia L., var. *pubescens* Palmer and Steyermark: Prairie pastures, and in open woodlands. Collections by W. H. Horr, July 5, 1930, Chautauqua and Montgomery County; R. L. McGregor 10854, Montgomery County; P. A. Rydberg and R. Imler, 416 Montgomery County.

Ludwigia palustris (L.) Ell., var. *americana* (DC.) Fern. and Grisc.: In a creek valley grassland. Collection by W. H. Horr E60, Wilson County.

Oenothera biennis L., var. *biennis:* In sandy soil of a dry exposed lake bed, and along a roadside bank in upland woods. Woodson County.

Oenothera biennis L., var. *canescens* T. and G.: In sandy soil of an upland woods. Woodson County.

Oenothera laciniata Hill: Open upland woods, prairie pastures, and flood plain woods.

Oenothera laciniata Hill, forma *grandiflora* (Wats.) Robinson: Reported for Greenwood County, Gates (1940).

Oenothera linifolia Nutt.: In sandy soil of an exposed lake bed, in shallow soil over surfacing sandstone of a prairie gully, and in an overgrazed pasture.

Oenothera missouriensis Sims, var. *missouriensis:* Prairie pastures, and rocky prairie gullies. All counties except Greenwood and Montgomery.

Oenothera missourienses Sims, var. *incana* Gray: Reported for Elk, Greenwood, and Montgomery counties, Gates (1940).

Oenothera serrulata Nutt.: Rocky prairie pastures and gullies.

Oenothera speciosa Nutt.: Prairie pastures, gullies, roadsides, and rocky banks in low prairie woodlands.

Oenothera triloba Nutt.: Overgrazed pasture, roadsides, and on a rocky wooded slope. Wilson and Woodson counties.

Stenosiphon linifolius (Nutt.) Britt.: Reported for Elk, Greenwood, and Wilson counties.

HALORAGACEAE

Myriophyllum pinnatum (Walt.) BSP.: In a prairie pasture pond, and in a prairie woodland marsh. Montgomery and Woodson counties.

UMBELLIFERAE

Chaerophyllum procumbens (L.) Crantz.: Reported for Montgomery County, Gates (1940).

Chaerophyllum tainturieri Hook: Roadsides, borders of low woodlands, fields, and waste places.

Cicuta maculata L.: Flood plain woods, in moist soil bordering a marsh, and waste fields.

Conium maculatum L.: Roadsides, and low woods. Woodson County.

Cryptotaenia candensis (L.) DC.: Reported for Woodson County, Gates (1940).

Daucus carota L.: Roadsides, fields, and waste places. Woodson County.

Eryngium leavenworthii T. and G.: Overgrazed pastures, prairie gullies, and waste places. Chautauqua, Wilson, and Woodson counties.

Eryngium yuccifolium Michx.: Prairie pastures, hilltops and slopes. All counties except Elk and Montgomery.

Lomatium foeniculaceum (Nutt.) C. and R.: Rocky prairie pastures, and in sandy soil of roadside banks. Woodson County.

Osmorphiza longistylis (Torr.) DC., var. *villicaulis* Fern.: Reported for Chautauqua and Greenwood counties, Gates (1940).

Perideridia americana (Nutt.) Reichenb.: Reported for Montgomery County, Gates (1940).

Polytaenia nuttallii DC.: Roadsides, rocky overgrazed prairie pastures, and in shallow soil over sandstone outcrops of an upland wooded gully.

Ptilimnium nuttallii (DC.) Britt.: Grazed and ungrazed prairies. Chautauqua and Woodson counties.

Sanicula canadensis L.: Creek bank, and flood plain woods.

Sanicula gregaria Bickn.: Reported for Greenwood County, Gates (1940).

Spermolepis inermis (Nutt.) Math. and Const.: Reported for Elk, Greenwood, and Montgomery counties.

Thaspium barbinode (Michx.) Nutt.: In a wet roadside ditch in lowland. Woodson County.

Torilis japonica (Hout.) DC.: Roadside ditch bank, open creek woods, and waste places. Wilson and Woodson counties.

Zizia aurea (L.) Koch: Creek valley thicket, flood plain woods, wooded prairie gullies, and creek banks. Woodson County.

CORNACEAE

Cornus drummondii C. A. Meyer: Flood plain woods, wooded gullies, and upland wooded hillsides.

Cornus obliqua Raf.: Open upland woods, wooded gullies, and open flood plain woods.

Cornus stolonifera Michx.: In a rocky wooded gully in upland, and in flood plain woods. Woodson County.

PRIMULACEAE

Androsace occidentalis Pursh: In sandy soil of open oak woods, and upland prairie woodlands. Woodson County.

Dodecantheon meadia L., var. *meadia:* In shallow soil over sandstone outcrops of an open oak woods. Found once, in Elk County.

Dodecatheon meadia L., var. *meadia*, forma *album* Macbr.: In shallow soil over sandstone outcrops of an open oak woods. Found once, in Elk County.

Dodecatheon meadia L., var. *brachycarpum* (Small) Fassett.: In sandy soil of an open scrub oak woods. Rare. Collection by W. H. Horr E159, Montgomery County.

Samolus parviflorus Raf.: In moist soil under a sandstone ledge in an open oak woods. Found once, in Chautauqua County.

SAPOTACEAE

Bumelia lanuginosa (Michx.) Pers., var. *oblongifolia* (Nutt.) Clark: Rocky prairie woodlands, and rocky gullies of upland woods.

EBENACEAE

Diospyros virginiana L.: Dry sandy soil in open woods, flood plain woods, creek valley thickets, and low prairie woodlands.

OLEACEAE

Fraxinus americana L.: Flood plain woods, wooded gullies, and upland wooded hillsides.

Fraxinus pennsylvanica Marsh., var. *subintegerrima* (Vahl.) Fern.: Flood plain woods, prairie woodlands, and upland wooded hillsides.

Fraxinus quadrangulata Michx.: Creek banks, wooded gullies, and lower slopes of upland wooded hillsides. Elk, Chautauqua, and Montgomery counties.

GENTIANACEAE

Centaurium texense (Griseb.) Fern.: Edge of dry limestone ledges in bluestem pastures. Collections by R. L. McGregor 1159, Montgomery County; 10862, Wilson County.

Gentiana puberula Michx.: Prairie pasture, and in open prairie woodland. Two collections, from Woodson County.

Sabatia campestris Nutt.: Sandy soil of an open wooded hillside and in a prairie woodland. Collections by R. L. McGregor 10830, Chautauqua County; 3421, Greenwood County; P. A. Rydberg and R. Imler 408, Montgomery County.

APOCYNACEAE

Apocynum cannabinum L., var. *cannabinum:* In sandy soil of open upland wooded hillsides, wet roadside ditches, border of prairie pasture ponds, in sandy soil of a lake shore, and prairie pastures.

Apocynum cannabinum L., var. *pubescens* (Mitchell) DC.: In sandy soil of a prairie pasture. Collection by W. H. Horr, June 6, 1930, Chautauqua County.

Apocynum sibiricum Jacq., var. *sibiricum:* Reported for Chautauqua and Wilson counties, Gates (1940).

Apocynum sibiricum Jacq., var. *cordigerum* (Greene) Fern.: Reported for Elk County, Gates (1940).

ASCLEPIADACEAE

Asclepias amplexicaulis Sm.: Reported for Chautauqua County, Gates (1940).

Asclepias asperula (Dcne.) Woodson, subsp. *capricornu* (Woodson) Woodson: Prairie pasture. Collection by R. L. McGregor 4295, Wilson County.

Asclepias hirtella (Pennell) Woodson: Roadside, low prairie pasture, and waste places. Woodson County.

Asclepias incarnata L.: Reported for Woodson County, Gates (1940).

Asclepias stenophylla A. Gray: Low prairie pastures, and rocky open hillsides. Elk, Greenwood, and Wilson counties.

Asclepias sullivantii Engelm. ex A. Gray: Prairie pastures, prairie woodlands, and open wooded hillsides. Collections by W. H. Horr, July 5, 1930, July 12, 1930, Chautauqua County; W. H. Horr and L. H. Franklin, E261, Wilson County.

Asclepias syriaca L.: Prairie pastures, wooded ravines, and border of a low woods. Greenwood and Woodson counties.

Asclepias tuberosa L.: Low prairie pastures, fields, and roadsides.

Asclepias tuberosa L., forma *lutea* Clute: In a low prairie pasture. Found once, in Chautauqua County.

Asclepias verticillata L.: Low prairie hay fields, in shallow soil over surfacing limestone of a prairie ravine, prairie pastures, and open upland woods.

Asclepias viridiflora Raf., var. *virdiflora:* Prairie pastures, rocky prairie gullies, and open wooded hillsides. Greenwood and Wilson counties.

Asclepias viridiflora Raf., var. *lanceolata* (Ives) Torr.: Dry bluestem prairie hillside. Collection by R. L. McGregor 10241, Wilson County.

Asclepias viridis (Walt.) Gray: Creek valley grassland, prairie pasture, roadsides, rocky banks in prairie woodlands, and in prairie gullies. Greenwood, Wilson, and Woodson counties.

Cynanchum laeve (Michx.) Pers.: Reported for Chautauqua, Elk, and Woodson counties, Gates (1940).

CONVOLVULACEAE

Convolvulus arvensis L.: Roadsides, fields, and waste places.

Convolvulus incanus Vahl.: Reported for Woodson County, Gates (1940).

Convolvulus pellitus Ledeb., forma *anestius* Fern.: Roadside ditch bank. Collection by J. L. Wilson, June 8, 1951, Wilson County.

Convolvulus sepium L.: Roadsides, fields, banks of prairie gullies, and waste places.

Cuscuta cuspidata Engelm.: Reported for Woodson County, Gates (1940).

Cuscuta glomerata Choisy: Reported for Elk, Greenwood, Montgomery and Chautauqua counties, Gates (1940).

Cuscuta pentagona Engelm.: Growing over low vegetation in a low open woodland. Collection by P. A. Rydberg and R. Imler 460, Montgomery County.

Evolvulus nuttallianus Schultze: In shallow soil on a limestone plateau, and rocky open wooded hillsides. Elk, Wilson, and Montgomery counties.

Ipomoea coccinea L.: In sandy soil bordering a cultivated field. Collection by W. H. Horr and R. L. McGregor E424, Montgomery County.

Ipomoea hederacea (L.) Jacq.: In sandy soil of a dry lake bed, low open woodlands, roadsides, fields, and waste places.

Ipomoea lacunosa L.: In sandy soil of an exposed lake bed. Collection by R. L. McGregor 3159, Woodson County.

Ipomoea pandurata (L.) G. F. W. Mey: Creek valley thicket, growing over low shrubs of flood plain woods, and waste places.

Ipomoea purpurea (L.) Roth.: Growing over low vegetation of a field bordering a flood plain woods. Woodson County.

POLEMONIACEAE

Phlox divaricata L., var. *laphamii* (Wood) Wherry: Flood plain woods, and open wooded hillsides. Chautauqua and Woodson counties.

Phlox divaricata L., var. *laphamii* (Wood) Wherry, forma *candida* Palmer and Steyermark: Bank of a creek below a wooded cliff. Found once, seven miles southwest of Yates Center, Woodson County.

Phlox oklahomensis Wherry: In shallow soil over surfacing limestone in a prairie pasture. Collection by R. L. McGregor 9051, Chautauqua County, 9052, Elk County.

Phlox pilosa L., subsp. *pilosa:* Prairies, and prairie woodlands. Chautauqua, Montgomery, and Wilson counties.

Phlox pilosa L., subsp. *ozarkana* Wherry: Prairie hay fields, pastures, and prairie woodlands. All counties except Elk and Greenwood.

HYDROPHYLLACEAE

Ellisia nyctelea L.: Flood plain woods, wooded gullies, and upland wooded hillsides. Chautauqua and Woodson counties.

Phacelia hirsuta Nutt.: Reported for Chautauqua and Wilson counties, Gates (1940).

BORAGINACEAE

Cynoglossum officinale L.: Reported for Chautauqua and Greenwood counties, Gates (1940).

Hackelia virginiana (L.) I. M. Johnston: In a prairie thicket. Collection by W. H. Horr, July 11, 1930, Woodson County.

Heliotropium tenellum (Nutt.) Torr.: In rocky prairie gullies, waste places, and prairie pasture hillsides.

Lappula echinata Gilib.: Open prairie woodlands. Woodson County.

Lappula redowskii (Hornem.) Greene: Reported for Wilson County, Gates (1940).

Lithospermum arvensis L.: Along the fence row in a prairie pasture. Woodson County.

Lithospermum incisum Lehm.: Prairie pastures, roadsides, and open prairie woodlands. Elk, Chautauqua, and Woodson counties.

Myosotis verna Nutt.: Sandy soil of open scrub oak woods, and in prairie woodlands. Chautauqua, Greenwood, and Wilson counties.

Onosmodium hispidissimum Mackenz.: Reported for Greenwood County, Gates (1940).

Onosmodium occidentale Mackenze: Rocky prairie pastures, and prairie woodlands. Montgomery and Wilson counties.

VERBENACEAE

Lippia lanceolata Michx., var. *reconita* Fern. and Grisc.: Low prairie pastures, stream and creek banks, and flood plain woods.

Verbena blanchardi Moldenke: Rocky overgrazed pastures. Rare. Woodson County.

Verbena bracteosa Michx.: Fields, waste places, and pastures. Woodson County.

Verbena canadensis (L.) Britton: Rocky prairie pastures, roadsides, open woods, and prairie woodlands. Frequent.

Verbena hastata L.: Rocky prairie pasture. Found once, in Woodson County.

× *Verbena moechina* Moldenke: Prairie pasture, and on an open wooded hillside. Collections by W. H. Horr, July 28, 1930, Greenwood County; P. A. Rydberg and R. Imler 434, Montgomery County.

× *Verbena rydbergii* Moldenke: Overgrazed prairie pastures, prairie woodlands, and waste places. Chautauqua and Woodson counties.

Verbena simplex Lehm.: Prairie pastures, rocky prairie woodlands, and open oak woods.

Verbena stricta Vent.: Rocky prairie gullies, overgrazed pastures, fields, and open flood plain woods.

Verbena urticifolia L.: Creek valley thickets, low prairie pastures, flood plain woods, and waste places.

LABIATAE

Agastache nepetoides (L.) Ktze.: Reported for Woodson County, Gates (1940).

Blephilia hirsuta (Pursh) Benth.: Creek valley thicket. Collection by W. H. Horr, E144, Wilson County.

Glechoma hederacea L., var. *micrantha* Moricand: Reported for Chautauqua County, Gates (1940).

Hedeoma hispida Pursh: Prairie pasture gullies, low pastures, flood plain woods, and rocky open woods.

Hedeoma pulegioides (L.) Pers.: Reported for Wilson County, Gates (1940).

Isanthus brachiatus (L.) BSP.: Creek banks, moist prairie gullies, and flood plain woods. Wilson and Woodson counties.

Lamium amplexicaule L.: Roadsides, low prairie woodlands, banks of wooded gullies.

Lamium purpureum L.: Low woodland creek banks, roadsides, and borders of fields. Woodson County.

Leonurus marrubiastrum L.: In shallow soil over surfacing limestone in a prairie pasture. Found once, in Woodson County.

Lycopus americanus Muhl., var. *scabrifolius* Fern.: In sandy soil of a dry lake bed, and open woodlands. Collection by R. L. McGregor 4110, Woodson County.

Marrubium vulgare L.: Flood plain woods. Collection by W. H. Horr, July 11, 1930, Woodson County.

Mentha arvensis L., var. *villosa* (Benth.) S. R. Stewart, forma *glabrata* (Benth.) S. R. Stewart: Reported for Greenwood County, Gates (1940).

Monarda citriodora Cerv.: Rocky prairie slopes, and prairie woodlands.

Monarda fistulosa L., var. *mollis* (L.) Benth.: Prairie hay fields, pastures, and prairie woodlands.

Monarda russeliana Nutt, ex Sims: Reported for Woodson County, Horr and McGregor (1949).

Nepeta cataria L.: Fields and waste places. Collections by W. H. Horr, July 11, 1930, Woodson County; July 12, 1930, Wilson County.

Physostegia intermedia (Nutt.) Engelm. and Gray: Prairie pasture hillside. Collection by W. H. Horr, July 5, 1930, Chautauqua County.

Physostegia virginiana (L.) Benth.: In a rocky prairie pasture. Found once, in Woodson County.

Prunella caroliniana Mill: Creek valley thicket, creek banks, and flood plain woods. Chautauqua, Montgomery, and Woodson counties.

Pycnanthemum tenuifolium Schrad.: Rocky prairie gullies, prairie pasture slopes, and low prairie woodlands.

Salvia azurea Lam., var. *grandiflora* Benth.: Prairie pastures, rocky prairie woodlands, wooded gullies, and roadsides.

Salvia reflexa Hornem.: Reported for Greenwood County, Gates (1940).

Scutellaria incana Biehler: Prairie hay field. Collection by B. L. Wagenknecht 1823, Chautauqua County.

Scutellaria lateriflora L.: Reported for Woodson County, Gates (1940).

Scutellaria ovata Hill: Reported for Chautauqua County, Gates (1940).

Scutellaria parvula Michx., var. *parvula:* Prairie hay fields, pastures, and open prairie woodlands. Montgomery and Woodson counties.

Scutellaria parvula Michx., var. *australis* Fassett.: Prairie hay fields and pastures. Woodson County.

Scutellaria parvula Michx., var. *leonardii* (Epling) Fern.: Grazed and ungrazed prairies, and rocky prairie woodlands. All counties except Elk and Montgomery.

Stachys palustris L.: On a creek bank, and in flood plain woods. Collections by W. H. Horr, July 5, 1930, Montgomery County; July 12, 1930, Wilson County.

Stachys tenuifolia Willd.: On a wooded creek bank. Found once, in Woodson County.

Teucrium canadense L., var. *virginicum* (L.) Eat.: Rocky prairies, low prairie woodlands, roadsides, and border of fields.

SOLANACEAE

Chamaesaracha conioides (moric.) Britt.: Reported for Woodson County, Gates (1940).

Datura stramonium L.: Roadsides, field, and waste places.

Physalis heterophylla Nees: Along the border of a flood plain woods. Woodson County.

Physalis pubescens L.: Prairie pasture. Collection by R. L. McGregor 10857, Woodson County.

Physalis pumila Nutt.: Low prairie pastures, rocky upland open woods, and waste places. Greenwood, Montgomery, and Wilson counties.

Physalis virginiana Mill.: Overgrazed pastures, in sandy soil of an exposed lake bed, rocky waste places, and roadsides.

Solanum americanum Mill.: Overgrazed pastures, fields, and low open woods. Woodson County.

Solanum carolinense L.: Waste places, overgrazed pastures, fields, and roadsides.

Solanum carolinense L., forma *albiflorum* (O. Ktze.) Benke.: Roadsides, fields, waste places, and overgrazed pastures.

Solanum elaeagnifloium Cav.: Reported for Woodson County, Gates (1940).

Solanum interius Rydb.: Reported for Woodson County, Gates (1940).

Solanum rostratum Dunal: In sandy soil of dry lake bed, roadsides, fields, and overgrazed pastures. Frequent.

SCROPHULARIACEAE

Bacopa rotundifolia (Michx.) Wettst.: In sandy soil of dry lake bed, in a temporary water hole in a prairie pasture, and in moist depressions in fields. Wilson and Woodson counties.

Buchnera americana L.: Rocky prairie gullies, and low prairie woodlands. Collections by W. H. Horr, July 5, 1930, Montgomery County; July 12, 1930, Wilson County; July 10, 1930, Woodson County; R. L. McGregor 4457, Elk County; 2393, Montgomery County.

Castilleja sessiliflora Pursh.: Rocky prairie hay field. Rare. Collection by R. L. McGregor 10259, Wilson County.

Collinsia violacea Nutt.: In sandy soil of open scrub oak wooded hillsides, and prairie woodlands. Collections by W. H. Horr E123, Wilson County; R. L. McGregor 9046, Chautauqua County; 9034, Montgomery County; 9030a, Wilson County; 9011, Woodson County.

Conobea multifida (Michx.) Benth.: Rocky scrub oak woods, prairie pastures, sandy soil of a dry lake bed, and prairie woodlands.

Gerardia aspera Dougl.: Reported for Greenwood, Montgomery, Wilson, and Woodson counties, Gates (1940).

Gerardia auriculata Michx.: In a rocky prairie pasture swale. Collection by R. L. McGregor 5237, Montgomery County.

Gerardia densiflora (Benth.) Pennell: Reported for Elk and Woodson counties, Gates (1940).

Gerardia skinneriana Wood: Prairie pastures, wooded gullies, open woods, and prairie woodlands. Woodson County.

Gerardia tenuifolia Vahl., var. *parviflora* Nutt.: Reported for Woodson County, Gates (1940).

Gratiola virginiana L.: In a moist prairie gully. Montgomery and Woodson counties.

Linaria canadensis (L.) Dumont, var. *texana* (Scheele) Pennell: Wooded gully, open upland woods, prairie pastures, and sandy soil of roadsides. Chautauqua and Woodson counties.

Lindernia anagallidea (Michx.) Pennell: Rocky prairie hillside, and in sandy soil of a dry lake bed. Woodson County.

Lindernia dubia (L.) Pennell: In sandy soil of an exposed lake bed, and open upland woods. Collections by W. H. Horr, July 5, 1930, Chautauqua and Montgomery counties; R. L. McGregor 3147, Woodson County.

Mimulus alatus Ait.: In moist soil on the bank of an upland wooded gully, creek bottoms, and wet ditch banks. Woodson County.

Pedicularis canadensis L.: Reported for Chautauqua County, Gates (1940).

Penstemon cobaea Nutt.: Rocky prairie slopes, and prairie woodlands.

Penstemon digitalis Nutt.: Reported for Montgomery and Wilson counties, Gates (1940).

Penstemon tubaeflorus Nutt.: Prairie pastures, rocky wooded gullies, and prairie woodlands.

Scrophularia marilandica L.: Prairie pasture. Collection by W. H. Horr, July 12, 1930, Wilson County.

Seymeria macrophylla Nutt.: Open scrub oak woods, and in sandy soil below a wooded cliff. Woodson County.

Verbascum blattaria L.: Rocky overgrazed pastures, and prairie woodlands.

Verbascum blatteria L., forma *albiflora* (Don) House: In overgrazed pastures. Collections by R. L. McGregor 4323, Montgomery County; 4288, Wilson County.

Verbascum thapsus L.: Rocky prairie pastures, waste places, and borders of fields.

Veronica arvensis L.: Open banks of wooded gullies, and in prairie pastures. Woodson County.

Veronica peregrina L., var. *peregrina*: Banks of prairie pasture ponds, lake shore in upland woods, and in moist gullies. Woodson County.

Veronica peregrina L., var. *xalapensis* (HBK.) St. John and Warren: In open upland woods, in sandy soil of a dry lake bed, and in a wooded prairie gully. Woodson County.

Veronica angalis-aquatica L.: Along the edge of a low woodland water hole. Found once, in Woodson County.

BIGNONIACEAE

Campsis radicans (L.) Seem: Growing over low vegetation along a river bank, and in a thicket of a prairie woodland. Montgomery and Woodson counties.

Catalpa speciosa Warder: Flood plain woods, fields, and invaded woods of prairies.

MARTYINACEAE

Proboscidea louisianica (Mill.) Thell.: Reported for Chatuauqua County, Gates (1940).

OROBANCHACEAE

Orobanche ludoviciana Nutt.: Reported for Greenwood County, Gates (1940).

Orobanche uniflora L.: Reported for Chautauqua, Montgomery, and Woodson counties, Gates (1940).

LENTIBULARIACEAE

Utricularia gibba L.: In the water of a low prairie woodland marsh. Woodson County.

ACANTHACEAE

Dicliptera brachiata (Pursh) Spreng: Moist soil along a river bank. Collection by R. L. McGregor 5735, Wilson County.

Justicia americana (L.) Vahl.: In prairie streams, shallow creeks, and moist wooded gullies. All counties except Elk and Greenwood.

Ruellia humilis Nutt., var. *humilis:* Low prairies, prairie woodlands, open oak woods, and open flood plain woods.

Ruellia humilis Nutt., var. *expansa* Fern.: Low prairie hay fields. Woodson County.

Ruellia humilis Nutt., var. *frondosa* Fern.: Prairie gully, and in shallow soil over surfacing limestone in a prairie pasture. Collections by R. L. McGregor 4465, Elk County; 10865, Wilson County.

Ruellia humilis Nutt., var. *longiflora* (Gray) Fern.: Grazed and ungrazed prairies, and open prairie woodlands.

Ruellia strepens L.: Flood plain woods.

PHRYMACEAE

Phryma leptostachya L.: Along the border of a wooded prairie gully, open flood plain woods, and lowland thickets. Greenwood, Wilson, and Woodson counties.

PLANTAGINACEAE

Plantago aristata Michx.: In sandy soil of an exposed lake bed, prairie pastures, open grazed woods, roadsides, prairie woodlands, and waste places. Frequent.

Plantago lanceolata L.: Roadsides, fields, and waste places.

Plantago major L.: Waste places, and borders of fields. Woodson County.

Plantago purshii R. and S.: Prairie pastures, and prairie woodlands.

Plantago pusilla Nutt.: Open upland woods.

Plantago rhodosperma Dene.: Prairie pastures, lowland woods, and waste places. Greenwood and Woodson counties.

Plantago rugelii Dene.: Flood plain woods, creek valley thickets, and roadsides. Collections by W. H. Horr, July 5, 1930, Chautauqua and Montgomery counties; July 11, 1930, Woodson County.

Plantago virginica L.: Open upland woods, rocky prairie pastures, prairie gullies, and roadsides. Frequent.

RUBIACEAE

Cephalanthus occidentalis L.: Upland wooded gullies, rocky creek banks, rocky shore of lakes, and open flood plain woods.

Diodia teres Walt., var. *setifera* Fern. and Grisc.: Rocky prairie pastures, fields, waste places, and in sandy soil of an exposed lake bed.

Galium aparine L.: Flood plain woods, and lower slopes of upland woods. Chautauqua and Woodson counties.

Galium circaezans Michx., var. *hypomalacum* Fern.: Flood plain woods, collection by W. H. Horr, July 11, 1930, Woodson County.

Galium triflorum Michx.: Wooded prairie ravines, and flood plain woods. Greenwood and Woodson counties.

Galium virgatum Nutt.: Low woodlands, in shallow soil over surfacing limestone of a prairie hay field, and in overgrazed pastures. Collections by R. L. McGregor 10213, 4343, Montgomery County; 4292, 10255, Wilson County.

Hedyotis minima (Beck) T. and G.: In shallow soil over surfacing sandstone of prairie pastures, and in upland prairie woodlands.

Hedyotis minima (Beck) T. and G., forma *albiflora* Lathrop: In shallow soil over surfacing sandstone in a prairie bordered by scrub oak woods. Collected in one location four miles southwest of Yates Center, Woodson County.

Hedyotis nigricans (Lam.) Fosberg: Flood plain woods, prairie pastures, and open upland woods.

CAPRIFOLIACEAE

Lonicera dioica L., var. *glaucesens* (Rydb.) Butters: On a wooded limestone escarpment. Rare. Collections by R. L. McGregor 2404, 10841, Montgomery County.

Lonicera japonica thunb.: Rocky wooded thicket covered hillside near a farm site. Collection by R. L. McGregor 4315, Wilson County.

Lonicera prolifera (Kirchn.) Rehd.: Just below a wooded limestone escarpment. Rare. Collection by R. L. McGregor 10230, Montgomery County.

Sambucus canadensis L.: Wooded river bank, flood plain woods, and lowland thickets.

Symphoricarpos orbiculatus Moench.: Open flood plain woods, and upland scrub oak woods. Frequent.

Triosteum aurantiacum Bickn., var. *illinoense* (Wieg.) Palmer and Steyerm.: Reported for Wilson County, Gates (1940).

Triosteum perfoliatum L.: Reported for Chautauqua, Greenwood, and Wilson counties, Gates (1940).

Viburnum rufidulum Raf.: Open wooded hillsides, and wooded gullies and ravines.

VALERIANACEAE

Valerianella radiata (L.) Dufr., var. *radiata*: Moist prairie gullies, muddy banks of pasture ponds, wet roadside ditches, and low prairies. Montgomery and Woodson counties.

Valerianella radiata (L.) Durfr., var. *missouriensis* Dyal: In a deep depression of a prairie hay field. Collection by R. L. McGregor 10209, Woodson County.

Valerianella stenocarpa (Engelm.) Krock., var. *parviflora* Dyal: Reported for Wilson County, Gates (1940).

CUCURBITACEAE

Echinocystis lobata (Michx.) T. and G.: Reported for Greenwood and Wilson counties, Gates (1940).

Sicyos angulatus L.: In rich woodland bordering Neosho River, and in thickets of low woods. Greenwood and Wilson counties.

CAMPANULACEAE

Campanula americana L., var. *illinoensis* (Fresn.) Farw.: Flood plain woods, low fields, creek bank thickets, and open woodlands. Chautauqua and Woodson counties.

Lobelia cardinalis L.: In moist soil over surfacing sandstone of wooded gullies, and wooded creek banks.

Lobelia siphilitia L.: Flood plain woods. Found once, in Woodson County.

Lobelia spicata Lam., var. *leptostachys* (A. DC.) Mackenz. and Bush.: In sandy soil of an exposed lake bed, prairie gulches, and moist wooded gullies. Montgomery and Woodson counties.

Lobelia splendens Willd.: Flood plain woods. Collection by O. S. Fearing and G. Latham, Aug. 14, 1950, Wilson County.

Specularia biflora (R. and P.) Fisch. and Mey: Low prairie hay fields and pastures. Woodson County.

Specularia perfoliata (L.) A. DC.: Rocky prairie gullies, prairie pastures, creek banks, and low prairie woodlands.

Specularia leptocarpa (Nutt.) Gray: Rocky prairie pastures, in sandy soil of an exposed lake bed, and in prairie woodlands.

COMPOSITAE

Achillea lanulosa Nutt.: Prairie pastures, and prairie woodlands. Frequent.

Actinomeris alternifolia (L.) DC.: Moist wooded gullies, and open flood plain woods. Woodson County.

Ambrosia artemisiifolia L., var. *elatior* (L.) Descourtils: Wooded river bank, in sandy soil of a dry lake bed, fields, and wooded prairie gullies. Chautauqua, Wilson, and Woodson counties.

Ambrosia bidentata Michx.: Rocky prairie pasture. Collection by B. L. Wagenknecht 2239, Wilson County.

Ambrosia psilostachya DC., var. *coronopifolia* (T. and G.) Farw.: Overgrazed prairie pastures, and prairie woodlands.

Ambrosia simulans Shinners: Dry prairie pasture. Collection by W. H. Horr and R. L. McGregor E435, Woodson County.

Ambrosia trifida L., var. *trifida:* Wooded creek banks, waste field bordering river woods, wooded prairie gullies, and sandy soil of an exposed lake bed. Woodson County.

Ambrosia trifida L., var. *texana* Scheele: Dense creek woods. Found once, in Woodson County.

Antennaria campestris Rydb.: Reported for Elk and Chautauqua counties, Gates (1940).

Antennaria fallax Greene: In sandy soil of open scrub oak hillsides. Chautauqua and Woodson counties.

Antennaria neglecta Greene, var. *neglecta:* Sandy soil of open scrub oak woods, prairies, and prairie woodlands.

Antennaria neglecta Greene, var. *randii* (Fern.) Cron.: Sandy soil of a prairie hay field. Collection by R. L. McGregor 9049, Chautauqua County.

Antennaria plantaginifolia (L.) Richards: In shallow soil over sandstone outcrops of a scrub oak woods. Greenwood and Wilson counties.

Anthemis cotula L.: In sandy soil of a dry lake bed, roadsides, fields, and creek valley woodlands. Collections by W. H. Horr, July 11, 1930, Woodson County; R. L. McGregor 3185, Woodson County.

Arctium minus (Hill) Bernh.: Reported for Elk, Chautauqua, Greenwood, and Wilson counties, Gates (1940).

Artemisia ludoviciana Nutt., var. *ludoviciana:* In shallow soil over limestone surfacing of a prairie pasture. Collection by B. L. Wagenknecht 2191, Wilson County.

Artemisia ludoviciana Nutt., var. *mexicana* (Willd.) Fern.: In sandy soil of gully bank in a prairie hay field and a prairie pasture. Collections by R. L. McGregor 9818, Woodson County; W. H. Horr and R. L. McGregor E432, Montgomery County.

Aster anomalus Engelm.: In calcareous soil of a roadside ditch bordering a prairie pasture. Found once, in Woodson County.

Aster azureus Lindl.: Grazed and ungrazed prairies. Wilson and Woodson counties.

Aster azureus Lindl., forma *laevicaulis* Fern.: In sandy-clay soil of a scrub oak wooded hillside. Collection by R. L. McGregor 4085, Woodson County.

Aster ericoides L.: Rocky prairie pasture gulches, prairie hillsides, fields, and roadsides.

Aster laevis L.: Prairie hay fields, and on rocky banks in river woodlands. Greenwood and Woodson counties.

Aster oblongifolius Nutt.: In shallow soil over surfacing sandstone of open oak woods, and in prairie hay fields. Greenwood, Wilson, and Woodson counties.

Aster patens Ait.: Prairie pastures, open oak woods, and rocky prairie gullies. Montgomery and Woodson counties.

Aster pracaltus Poir.: Prairie pastures. Collections by B. L. Wagenknecht 1728, Montgomery County; 2242, Wilson County.

Aster sagittifolius Wendemeyer, var. *sagittifolius*: Open upland wooded hillside. Collection by B. L. Wagenknecht 2254, Wilson County.

Aster sagittifolius Wedemeyer, var. *drummondii* (Lindl.) Shinners: Prairie pastures, oak wooded hillsides, and rocky prairie gullies. Greenwood and Woodson counties.

Aster sericeus Vent.: Reported for Chautauqua, Elk, and Greenwood counties, Gates (1940).

Bidens bipinnata L.: Reported for Elk, Wilson, and Montgomery counties, Gates (1940).

Bidens cernua L., var. *elliptica* Wieg.: In sandy soil of an exposed lake bed. Collection by R. L. McGregor 4105, Woodson County.

Bidens frondosa L.: Wooded upland gullies, and in sandy soil of a dry lake bed. Wilson and Woodson counties.

Bidens polylepis Blake: Flood plain woods, prairie pastures, roadsides, prairie woodlands, and in sandy soil of a dry lake bed. Woodson County.

Boltonia latisquama Gray, var. *latisquama:* In a rocky wooded prairie gully. Collected once, in Woodson County.

Boltonia latisquama Gray, var. *recognita* Fern. and Grisc.: In a moist prairie gulch. Found once, in Woodson County.

Cacalia artiplicifolia L.: Reported for Greenwood and Wilson counties, Gates (1940).

Cacalia plantaginea (Raf.) Shinners: Prairie pastures, fields, and in shallow soil over limestone outcrops in prairie gullies.

Carduus nutans L.: Disturbed area of a prairie pasture. Collection by R. L. McGregor 4462, Elk County.

Centaurea cyanus L.: Prairie pasture, and open woodland in the Verdigris River flood plain. Chautauqua and Montgomery counties.

Chaetopappa asteroides DC.: In shallow soil over surfacing sandstone in open scrub oak woods. Chautauqua, Wilson, and Woodson counties.

Chrysanthemum leucanthemum L., var. *pinnatifidum* Lecoq. and Lamotte: On a creek bank, and in a low prairie pasture. Collections by W. H. Horr, June 28, 1930, Greenwood County; July 11, 1930, Woodson County.

Chrysopsis pilosa Nutt.: Light sandy soil of open scrub oak woods and prairie woodlands.

Chryopsis villosa (Pursh) Nutt., var. *villosa*: Light sandy soil along the border of a prairie hay field. Collection by B. L. Wagenknecht 1706, Montgomery County.

Chrysopsis villosa (Pursh) Nutt., var. *angustifolia* (Rydb.) Cronq.: In sandy soil of an open scrub oak woods. Found once, in Woodson County.

Chrysopsis villosa (Pursh) Nutt., var. *hispida* (Hook.) and Gray: In sandy soil of an open wooded hillside. Collection by R. L. McGregor 3184, Woodson County.

Cichorium intybus L.: Fields, roadsides, and pasture gullies. Wilson and Woodson counties.

Cirsium altissimum (L.) Spreng.: In sandy soil of open oak woods. Chautauqua and Woodson counties.

Cirsium undulatum (Nutt.) Spreng, var. *undulatum*: Rocky prairie pastures, prairie gullies, and fields.

Cirsium undulatum (Nutt.) Spreng, var. *undulatum*, forma *album* Farwell: In a rocky overgrazed pasture. Collected once, in Woodson County.

Cirsium undulatum (Nutt.) Spreng, var. *megacephalum* (Gray) Fern.: Prairie pasture. Collection by W. H. Horr, June 28, 1930, Greenwood County.

Conyza canadensis (L.) Cronq.: Border of flood plain woods, sandy soil of an open oak wood hillside, and in waste places. Chautauqua and Woodson counties.

Conyza ramosissima Cronq.: Creek valley thicket. Collection by W. H. Horr, July 12, 1930, Wilson County.

Coreopsis grandiflora Hogg.: In shallow soil over surfacing sandstone in upland prairie woodlands. Chautauqua County.

Coreopsis palmata Nutt.: Prairie pasture hillsides, rocky prairie gullies, open oak woods, and roadsides. Montgomery, Wilson, and Woodson counties.

Coreopsis tinctoria Nutt.: In sandy soil of open scrub oak woods. Chautauqua, Montgomery, and Woodson counties.

Dyssodia papposa (Vent.) Hichc.: Reported for all counties except Chautauqua, Gates (1940).

Echinacea angustifolia DC.: Prairie hay field hillsides, rocky banks of prairie gullies, and roadside banks.

Echinacea atrorubens Nutt.: Ungrazed prairies, rocky slopes of prairie woodland hillsides, and roadside banks.

Echinacea pallida Nutt.: Rocky banks in prairie pastures, roadside banks, and low prairie hay fields.

Eclipta alba (L.) Hassk.: In sandy soil of an exposed lake bed. Reported for Woodson County, McGregor and Volle (1950).

Erechtites hieracifolia (L.) Raf., var. *intermedia* Fern.: Reported for Woodson County, Gates (1940).

Erigeron annuus (L.) Pers.: Overgrazed prairie pastures, fields, and prairie woodlands. Wilson and Woodson counties.

Erigeron philadelphicus L.: In moist prairie pasture gulches, and wet roadside ditches. Chautauqua and Woodson counties.

Erigeron strigosus Muhl. ex Willd., var. *strigosus*: Prairie pastures, fields, roadsides, prairie woodlands, and waste places.

Erigeron strigosus Muhl. ex Willd., var. *beyrichii* (Fisch. and Mey) Gray: Flood plain woods, rocky roadside ditch, fields, rocky prairie pastures, and waste places. Montgomery and Woodson counties.

Eupatorium altissimum L.: Prairie pastures, thickets, and borders of woods. Woodson County.

Eupatorium perfoliatum L.: Reported for Chautauqua County, Gates (1940).

Eupatorium rugosum Houtt.: Reported for all counties except Greenwood and Chautauqua, Gates (1940).

Eupatorium rugosum Houtt., forma *villicaule* Fern.: Flood plain woods, along borders of low woodlands, and wooded gullies. Montgomery and Woodson counties.

Eupatorium serotinum Michx.: In low prairie woodlands. Elk and Woodson counties.

Euthamia gymnospermoides Greene: Prairie pastures, and prairie woodlands. Woodson County.

Gaillardia pulchella Foug.: In shallow soil over surfacing limestone in a prairie pasture. Collection by R. L. McGregor 10360, Elk County.

Gnaphalium obtusifolium L.: In sandy soil of prairie pastures. Collections by W. H. Horr and R. L. McGregor E421, Montgomery County; B. L. Wagenknecht 2241, Wilson County.

Gnaphalium purpureum L.: In sandy soil of a dry lake bed. Collections by R. L. McGregor 3121, Woodson County.

Grindelia lanceolata Nutt.: Wasteland, roadsides, and fields. Collection by R. L. McGregor 5738, Wilson County.

Grindelia squarrosa (Pursh) Dunal.: Rocky prairie banks, and roadsides. Woodson County.

Helenium autumnale L., var. *autumnale*: In a moist wooded gully in a prairie pasture. Woodson County.

Helenium autumnale L., var. *canaliculatum* (Lam.) Torr. and Gray: Specimen in the Gray Herbarium. Hitchcock 737, Chautauqua County.

Helenium monatanum Nutt.: Prairie pasture hillside. Collection by W. H. Horr and R. L. McGregor E425, Montgomery County.

Helenium tenuifolium Nutt.: Low prairie woodlands, overgrazed pastures, and fields.

Helianthus annus L.: Roadside ditch banks, fields, sandy soil of dry lake bed, waste places, and prairie woodlands.

Helianthus grosseserratus Martens: Roadside ditch, borders of fields, and waste places. Chautauqua and Woodson counties.

Helianthus hirsuta Raf., var. *hirsuta*: In sandy soil of roadsides, and on a sandy bank in an open oak woods. Chautauqua, Montgomery, and Woodson Counties.

Helianthus hirsuta Raf., var. *stenophyllus* T. and G.: In sandy soil of a bank in an open scrub oak woods. Found once, in Woodson County.

Helianthus laetiflorus Pers., var. *rigidus* (Cass.) Fern.: In sandy soil of a prairie pasture gully, roadsides, railroad embankments, fields, and waste places. Montgomery, Wilson, and Woodson counties.

Helianthus leptocaulis (S. Wats.) Blake: Reported for Montgomery County, Gates (1940).

Helianthus maximiliani Schrad.: Roadside banks, fields, border of flood plain woods, and in sandy soil of an exposed lake bed. Wilson and Woodson counties.

Helianthus mollis Lam.: Fields, border of low woods, roadsides, prairie gullies, waste places, and railroad embankments.

Helianthus petiolaris Nutt.: Roadsides, waste places, fields, and railroad embankments. Woodson County.

Helianthus salicifolius A. Dietr.: In dry soil over limestone of pasture and roadside banks.

Helianthus tuberosus L.: Roadsides, border of flood plain woods, waste places, and fields.

Heliopsis helianthoides (L.) Sweet, var. *scabra* (Dunal) Fern.: Rocky prairie pasture bank, thickets, and borders of woods. Wilson and Woodson counties.

Hieracium gronovii L.: In sandy soil of open upland woods, rocky banks of wooded gullies, and in shallow soil over sandstone outcrops. Chautauqua and Woodson counties.

Hieracium longipilum Torr.: Low prairies, and prairie gullies. Montgomery, Wilson, and Woodson counties.

Hymenopappus corymbosus T. and G.: Moist prairie gulch, and on a rocky prairie hillside. Collections by R. L. McGregor 4326, Montgomery County; 4298, Wilson County.

Hymenopappus scabiosaeous L'Her.: Roadside bordering prairie pasture, flood plain woods, and rocky prairie pastures.

Iva ciliata Willd.: On a rocky bank in an open woods, border of woods, and rocky waste places. Woodson County.

Krigia dandelion (L.) Nutt.: Rocky prairie woodlands. Chautauqua County.

Krigia occidentalis Nutt.: Reported for Chautauqua County, Gates (1940).

Kuhnia eupatoriodes L., var. *corymbulosa* T. and G.: Grazed and ungrazed prairies, and rocky prairie woodlands. Greenwood, Montgomery, and Wilson counties.

Lactuca canadensis L.: Reported for all counties except Chautauqua and Wilson, Gates (1940).

Lactuca floridana (L.) Gaertn.: Flood plain woods, and in moist soil of a rocky wooded gully. Woodson County.

Lactuca ludoviciana (Nutt.) Riddell: Low open woods. Collection by W. H. Horr, July 5, 1930, Montgomery County.

Lactuca scariola L.: Low prairie woodlands, rocky waste places, roadsides, fields, and along the border of an overgrazed pasture. Chautauqua, Wilson, and Woodson counties.

Liatris aspera Michx.: In sandy soil of prairie pastures, roadsides, and prairie woodlands.

Liatris punctata Hook., var. *punctata*: Prairie woodlands, rocky prairie pastures, and roadsides. Woodson County.

Liatris punctata Hook., var. *nebraskana* Gaiser: Roadsides, prairie pastures, and borders of low woods. Woodson County.

Liatris pycnostachya Michx.: Prairie pastures, roadsides, prairie gullies, open scrub oak woods, and along edges of fields.

Liatris squarrosa (L.) Michx., var. *glabrata* (Rydb.) Gaiser: Roadsides, fields, waste places, and in open oak woods. Montgomery and Woodson counties.

Liatris squarrosa (L.) Michx., var. *hirsuta* Rydb. ex Gaiser: Upland wooded gully, prairie pastures, roadsides, and in sandy soil of prairie woodlands. Chautauqua, Montgomery, and Woodson counties.

Marshallia caespitosa Nutt.: In a prairie pasture bordering a wooded limestone escarpment. Collection by R. L. McGregor 3400, Montgomery County.

Parthenium hispidum Raf.: Prairie pasture hillsides. Collections by R. L. McGregor 10341, 10366, Elk County.

Prenanthes aspera Michx.: Reported for Elk, Montgomery, and Woodson counties, Gates (1940).

Prionopsis ciliata Nutt.: In clay soil along the fence row of a cultivated field. Collection by B. L. Wagenknecht 1810, Chautauqua County.

Pyrrhopappus carolinianus (Walt.) DC.: Low prairie woodlands, roadsides, open scrub oak woods, in sandy soil of an exposed lake bed, creek banks, and flood plain woods.

Ratibida columnifera (Nutt.) W. and S.: Prairie pasture hillsides, roadsides and prairie gullies. All counties except Greenwood and Wilson.

Ratibida pinnata (Vent.) Barnh.: Rocky prairie gullies, and low prairie woodlands. Wilson and Woodson counties.

Rudbeckia amplexicaulis Vahl.: Flood plain woods, and low prairie woodlands. All counties except Elk and Woodson.

Rudbeckia laciniata L.: Border of a flood plain woods. Collection by R. L. McGregor 5734, Wilson County.

Rudbeckia serotina Nutt.: Rocky prairie pastures, along the edge of flood plain woods, and roadsides. Chautauqua, Montgomery, and Woodson counties.

Rudbeckia triloba L.: Flood plain woods, and in moist soil at the border of a lake in upland woods. Woodson County.

Senecio obovatus Muhl., var. *rotundus* Britt.: In sandy soil of an oak wooded hillside. Found once, in Chautauqua County.

Senecio plattensis Nutt.: In rocky prairie gulches, prairie pastures, rocky wooded ravines in upland woods, and prairie woodlands.

Serina oppositifolia (Raf.) Ktze.: Roadside rocky banks, prairie pastures, moist prairie gulches, along the edge of pasture ponds, and gullies in woodlands. Woodson County.

Silphium laciniatum L.: Roadsides, fields, waste places, and along the border of flood plain woods.

Silphium perfoliantum L.: Along the edge of a flood plain woods. Collected once, in Woodson County.

Silphium speciosum Nutt.: Roadsides, rocky banks in wasteland, borders of low woods, and in rocky prairie gullies.

Solidago altissima L.: Roadsides, borders of woodlands, prairie pastures, and rocky prairie gullies.

Solidago flexicaulis L.: In moist soil of a bank in a flood plain woods. Collection by B. L. Wagenknecht 1815, Chautauqua County.

Solidago gigantea Ait., var. *leiophylla* Fern.: Along the edge of flood plain woods. Chautauqua and Woodson counties.

Solidago lindheimeriana Scheele: Reported for Elk County, Gates (1940).

Solidago missouriensis Nutt., var. *glaberrima* (Martens) Rosendahl.: Prairie pastures, roadsides, prairie woodlands, low prairie hay fields, and open scrub oak woods.

Solidago petiolaris Ait.: In a rocky gully of a prairie hay field. Collection by R. L. McGregor 9802, Greenwood County.

Solidago rigida L.: In sandy soil of prairie woodlands, rocky prairie gulches, roadsides, and waste places.

Solidago speciosa Nutt., var. *angustata* T. and G.: Moist prairie pasture gulch. Collection by W. H. Horr and R. L. McGregor E430, Chautauqua County.

Solidago ulmifolia Muhl., var. *ulmifloia:* In sandy soil of open scrub oak woods, prairies, wooded gullies, and roadsides. Frequent.

Solidago ulmifolia Muhl., var. *microphylla* Gray: In sandy soil of an open scrub oak woods. Collection by R. L. McGregor 10858, Montgomery County.

Sonchus asper (L.) Hill: Roadsides, fields, and waste places.

Taraxacum erythrospermum Andrz.: Roadside ditch banks, prairie gullies, overgrazed pasture, and fields.

Taraxacum officinale Wiggers: In moist prairie gullies, borders of woods, roadside banks and fields.

Thelesperma intermedium Rydb.: Prairie pastures, rocky prairie gullies, in sandy soil of open oak woods, and rocky prairie woodlands.

Tragopogon pratensis L.: Overgrazed prairie pasture. Montgomery and Woodson counties.

Verbesina virginica L.: Flood plain woods, and in sandy soil of an open scrub oak woods. Chautauqua and Woodson counties.

Vernonia baldwini Torr., var. *interior* (Small) Schub.: Fields, overgrazed pastures, waste places, grazed prairie woodlands, and roadsides.

Vernonia baldwini Torr., var. *interior* (Small) Schub. × *V. crinita* Raf.: Reported for Chautauqua, Montgomery, and Woodson counties, Gates (1940).

Vernonia crinata Raf.: Low prairie gullies, in sandy soil of stream and creek banks, and roadsides. Collections by W. H. Horr, July 5, 1930, Chautauqua County; July 12, 1930, Wilson County; O. S. Fearing and G. Latham, Aug. 11, 1950, Chautauqua County; B. L. Wagenknecht 1857, 1776, Chautauqua County; 1722, Montgomery County.

Vernonia fasciculata Michx., var. *fasciculata*: In sandy soil of upland prairie woodland, and along the border of a flood plain woods. Woodson County.

Vernonia fasciculata Michx., var. *corymbosa* (Schwein.) Schub.: Along the edge of a flood plain woods. Found once, in Woodson County.

Xanthocephalum dracunculoides (DC.) Shinners: Overgrazed pastures, rocky prairie gullies, and waste places.

SUMMARY

The Chautauqua Hills area is a physiographic province in Kansas. It lies between the Osage Plains on the east and the Flint Hills on the west. It is bordered on the north by the Illinoian Biotic Province. The Kansas State line in Chautauqua and Montgomery counties marks its southern boundary. This region is the northern limits of the Texan Biotic Province. The area is characterized by low rolling hills capped with sandstone and covered on the tops and upper slopes with a growth of *Quercus stellata* and *Q. marilandica,* along with *Q. velutina* and *Q. prinoides* which form an oak savanna. The soil is typically light and sandy and the oaks are relicts from a former moist phase of the climatic cycle that have been able to maintain themselves against the competition of the grasses by virtue of the favorable amount of water available in the sandy soil. Trees common in flood plains become admixed with the above on slopes and in gullies and ravines. Evi-

dence from early survey notes and tree ring counts establishes proof that the Chautauqua Hills were wooded before the time of settlement. The upland forests, however, were not as extensive or as dense as they are at present.

Prolonged protection from fire permitted the encroachment of upland trees into the surrounding prairie areas as far as the environment allowed. There is less prairie now than before settlement due to much of it being plowed for cultivation by the settlers. Many prairie areas which remain have had their original species replaced by less desirable grasses and by various weedy forbs. The tree species in the flood plains and uplands at the present time are essentially the same as before settlement. The rest of the present flora, however, is much different than that present before man brought his disturbing influence to the region.

This study was undertaken with the view in mind to present an account of the flora and ecology of the Chautauqua Hills of Kansas, along with a description of the area before settlement. Species percentage composition for the characteristic plants of the woodland and prairie is included along with an annotated list of 1,030 taxa of vascular plants for the area.

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PLATE 1

FIG. 1. Rolling prairie showing the Chautauqua Hills capped with scrub oak. Three miles north of Elk City, Montgomery County.

FIG. 2. Prairie woodland showing upland wooded hills in the background. Eight miles east of Elgin, Chautauqua County.

PLATE 2

FIG. 1. Prairie hilltop capped with a growth of scrub oak. Nine miles south, five miles west of Fredonia, Wilson County.

FIG. 2. Closer view of a wooded prairie hilltop of the Chautauqua Hills. Three miles north of New Albany, Wilson County.

PLATE 3

FIG. 1. Open scrub oak woods. Eight miles northeast of Sedan, Chautauqua County.

FIG. 2. Interior of the above woods.

PLATE 4

FIG. 1. Upper slope of an upland woods. Five miles west, four miles south of Yates Center, Woodson County.

FIG. 2. Lower part of the same slope.

PLATE 5

FIG. 1. Wooded hillside over limestone outside the border of the Chautauqua Hills. Five miles west of Syracuse, Montgomery County.

FIG. 2. Wooded hillside over sandstone in the Chautauqua Hills. Three miles southeast of Sedan, Chautauqua County.

PLATE 6

FIG. 1. Prairie in the Chautauqua Hills. Two miles south, three miles east of Toronto, Woodson County.

FIG. 2. Prairie slope. Four miles east of Sedan, Chautauqua County.

PLATE 7

FIG. 1. Ungrazed prairie in good condition, showing nearly continuous grass cover. Six miles north of Longton, Elk County.

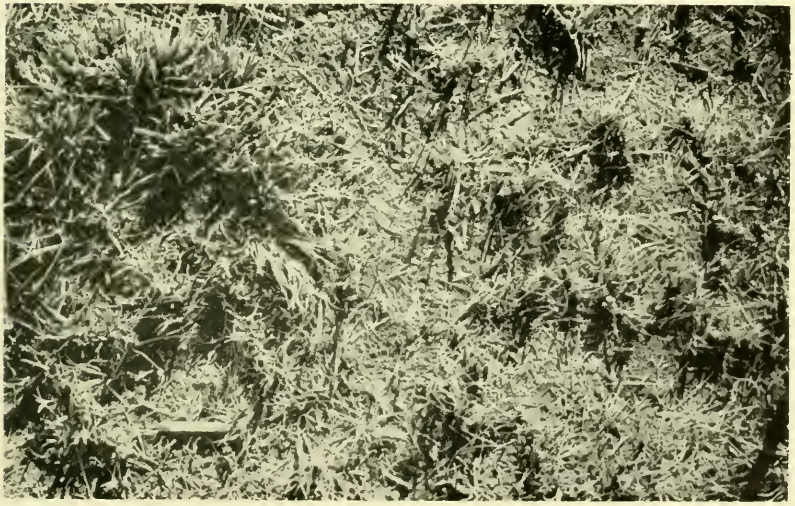

FIG. 2. Clipped vegetation of the above prairie showing extent of ground cover.

PLATE 8

FIG. 1. Grazed prairie in fair condition showing abundance of forbs. Five miles east of Sedan, Chautauqua County.

FIG. 2. Clipped vegetation of the above prairie showing extent of ground cover.

PLATE 9

FIG. 1. Grazed prairie in poor condition, showing invasion by weeds. Two miles northeast of Sedan, Chautauqua County.

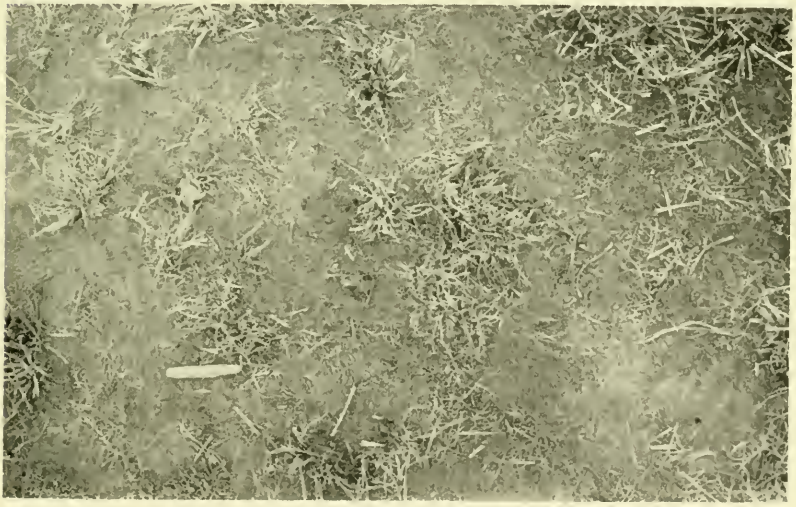

FIG. 2. Clipped vegetation of the above prairie showing extent of ground cover.

PLATE 10

FIG. 1. Flood plain woods of Fall river. One mile east of Fall river, Greenwood County.

FIG. 2. Interior of flood plain woods near the bank of Fall river. Five miles west of Fredonia, Wilson County.

PLATE 11

FIG. 1. Prairie woodland. Two miles north of New Albany, Wilson County.

FIG. 2. Prairie woodland showing a stand of *Quercus stellata* and *Q. marilandica.*

PLATE 12

FIG. 1. View of a small lake in the Chautauqua Hills. Five miles southwest of Elk City, Montgomery County.

FIG. 2. Wooded banks of Fall river. Five miles west of Fredonia, Wilson County.

PLATE 13

FIG. 1. Woodland marsh showing a colony of *Potamogeton gramineus* var. *myriophyllus* in the left foreground. One of the insect catching plants, *Utricularia gibba*, forms a dense growth under the water. Three miles east of Yates Center, Woodson County.

FIG. 2. Marsh in a low prairie with a colony of *Typha latifolia* in the middle foreground. Two miles east of Yates Center, Woodson County.

PLATE 14

FIG. 1. Temporary water hole in a low woodland with a colony of fruiting *Potamogeton nodosus* rising above the water. Three miles east of Busby, Elk County.

FIG. 2. View of a prairie water hole showing an extensive growth of *Spirodela polyrhiza* and other water plants. Seven miles east of Neosho Falls, Woodson County.

PLATE 15

FIG. 1. Upland wooded gully. Two miles northeast of Sedan, Chautauqua County.

FIG. 2. Temporary water hole in an upland gully. Two miles northeast of Sedan, Chautauqua County.

PLATE 16

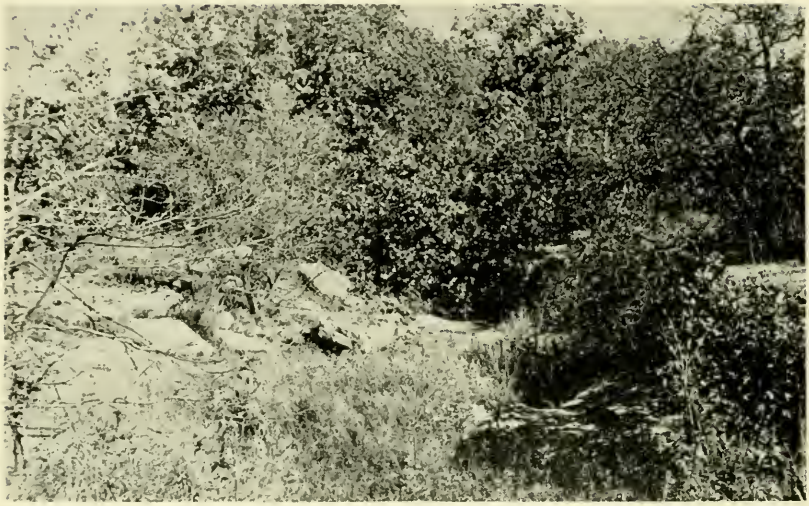

FIG. 1. Gully leading into a scrub oak woods. Two miles west of Yates Center, Woodson County.

FIG. 2. The same gully in the winter time.

PLATE 17

FIG. 1. Cliff above a creek showing sandstone outcrops and boulders. Six miles southwest of Yates Center, Woodson County.

FIG. 2. Same cliff in the winter.

PLATE 18

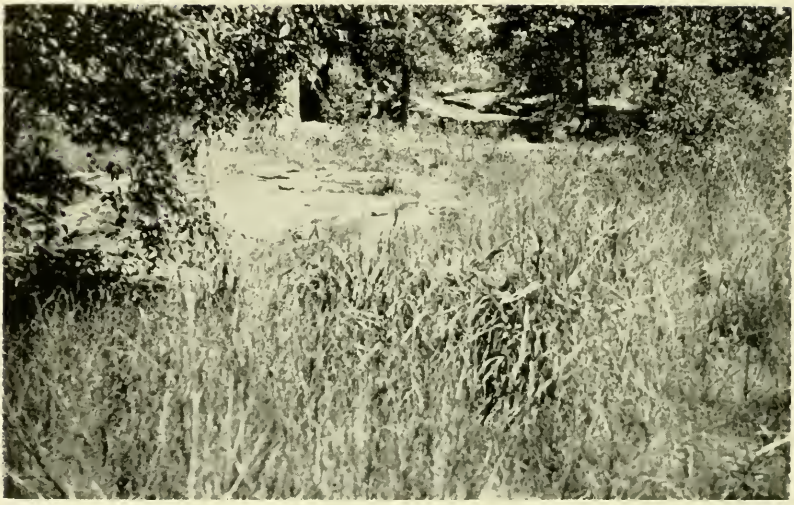

FIG. 1. Open upland wooded slope showing surfacing sandstone. Two miles northeast of Sedan, Chautauqua County.

FIG. 2. Sandstone outcrops of a wooded gully. Four miles southwest of Yates Center, Woodson County.

PLATE 19

FIG. 1. Stream in an upland wooded ravine. Eight miles north of Sedan, Chautauqua County.

FIG. 2. Wooded banks of a lowland creek. Two miles south of Toronto, Woodson County.

PLATE 20

FIG. 1. Roadside habitat of an upland woods. Two miles south, five miles east of Toronto, Woodson County.

FIG. 2. Prairie roadside habitat. Five miles southwest of Yates Center, Woodson County.

PLATE 21

FIG. 1. Abandoned field showing weedy growth of species of *Chenopodium*, *Ambrosia*, and *Lactuca*. Two miles south of Toronto, Woodson County.

FIG. 2. Pasture field showing characteristics of waste places. Two miles north of Hale, Chautauqua County.

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A Subgeneric Revision of the Genus *Osmia* in the Western Hemisphere (Hymenoptera: Megachilidae)[1]

BY

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ABSTRACT. In this paper the species of *Osmia* found in the Western Hemisphere are placed in eleven subgenera and a key to the subgenera is given, together with descriptions of them. The group commonly placed in a separate genus, *Diceratosmia*, is included in *Osmia*. The following new subgeneric names are proposed: *Chenosmia*, *Euthosmia*, *Trichinosmia*. From an extensive analysis of characters, it is concluded that in many features *Diceratosmia* is more primitive than other subgenera and that most of the subgenera must have arisen from *Diceratosmia*-like ancestors.

INTRODUCTION

This paper is a systematic revision, to the subgeneric level, of megachiline bees of the genus *Osmia* of the Western Hemisphere. The purpose of the study was to determine the natural groups and their limits and interrelationships within the genus.

Of approximately 213 species (approximately 25,000 specimens) studied, 140 occur in the New World. The rest are from the Old World and only a small fraction of the latter belong within the genus *Osmia* as defined by American authors (see discussion of the Old World Species). On the basis of the American species, the genus has been divided into eleven subgenera. In selecting the subgeneric characters, each of the specific characters used by previous authors, as well as new ones found in the present study, has been examined and evaluated with respect to all species. An effort has been made to detect variations (specific, subspecific and individual) of each character chosen.

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Sandhouse (1939) gave a comprehensive subgeneric classification of American forms of the genus while both American and Old World subgenera were briefly treated by Michener (1941). Sandhouse recognized six subgenera comprising 130 New World species. *Nothosmia* Ashmead, the largest of her subgenera, included 73 species. It was an artificial category containing a number of distinct groups of species. Other workers (Hurd and Michener, 1955:218) have recognized that a further revision was needed in order properly to treat the large number of species. I have distinguished six different subgenera among the species classified under *Nothosmia* by Sandhouse. Three American species assigned to the Old World subgenus *Melanosmia* Schmiedeknecht by Sandhouse (1939:33) have been removed from that subgenus. Of these three species, *O. bucephala* is the type species of the re-established subgenus *Centrosmia* Robertson to which *O. nigriventris* also belongs and in which fall various species of Sandhouse's *Nothosmia*. The other species of Sandhouse's *Melanosmia, O. inermis,* has been transferred to the subgenus *Chenosmia,* from typical members of which it differs only by nonmetallic coloration. The subgenus *Melanosmia,* thus, does not occur in the New World.

The genus *Diceratosmia* of authors (Robertson, 1903:166, Michener, 1949b:258) has been reduced to a subgenus of *Osmia* because of the intergradation of characters found in *O.* (*Nothosmia*) *marginata* and other species. Details regarding this change are discussed elsewhere in this paper.

DESCRIPTIVE METHODOLOGY

The morphological terminology used is mainly from Michener (1944). Specialized expressions are explained as follows: The impunctate band of the clypeal margin is termed "broad" when half or more than half as wide as the maximum width of the scape, and "narrow", when less than half as wide as the maximum width of the scape. These measurements are taken in the lateral part of the clypeal margin, not in the center. Punctations of the clypeus, when described, are those of the upper part of the clypeus. The width of the eye includes the darker area on the outer side and the inner carina on the mesal side measured at the maximum width of the eye. The width of the genal area is also taken at the point of maximum breadth. The measurements of the width of the eye and the genal area are taken from separate lateral views to give the maxi-

mum width of each. The mandible of the male bears two teeth, the upper and the lower. In the female there are three or four teeth. These are numbered in the following order: tooth 1, the uppermost; tooth 2; tooth 3; tooth 4, the lowermost. The second tooth is often small, rudimentary, almost confluent with the first tooth, or even absent in certain subgenera. When this tooth is absent, the tooth following the first tooth is termed the third tooth. The distances between the first tooth and the third and between the third and the fourth teeth are taken from the tip of one tooth to the tip of the other. A few of the mandibular drawings, such as *Osmia glauca*, are based on worn mandibles. In such cases the supposed lengths of the original teeth have been shown by dotted lines.

The inner anterior angle of the hypostomal carina is often broadly rounded. In the descriptions of the carina the expression "at the angle" means the hypothetical apex of the angle that would be made by extending the straight portions of the carina and "behind angle" means anywhere posterior to the apex (real or imaginary) of the angle. In the forewing of the male vein A is that part of the vein M between the first transverse cubital and the first recurrent vein, and vein B is that part of vein M between the second recurrent and the second transverse cubital. The width of the hind basitarsus is measured at the point of the maximum width. The first metasomal tergum is the second abdominal segment, *i. e.*, the one posterior to the propodeum; other terga and sterna are numbered accordingly.

In the figures the characters of one or two representative species are usually drawn for each subgenus. Also, certain characters have been drawn for a few species which differ from the representative species.

In subgeneric descriptions, when a particular character is found to be unique for a group and not to occur in any other subgenus, it is italicized and not mentioned in the descriptions of the other subgenera.

In the synonymies, references to the following works have been omitted: Dalla Torre (1896), Michener (1951, in Muesebeck, et al.) and Sandhouse (1943).

The drawings are all diagrams; they omit many details of no importance at the subgeneric level. It should be pointed out that Sandhouse (1939) gives many excellent drawings, for example, of genitalia and sterna of males, which should be used in conjunction with the present work.

PHYLOGENY

In the discussion of relationships that follows, the words "primitive" and "derived" or "modified" are used to describe the condition of the morphological features. The words "generalized" and "specialized" are used to describe the condition of species or groups of species judged by an average of all of the features studied. For instance, a subgenus is generalized if it has a large number of primitive characters and specialized if it has a large number of derived characters.

Table I was prepared to contrast primitive and derived characters useful among *Osmia* species, primitiveness being judged by similarity of the character to features found among other genera and among families of more wasplike bees. Often two or more derived conditions exist in relation to a single primitive one.

In postulating the phylogenetic arrangement of the genera of *Osmiini*,[2] Michener (1941:151) rightly assumed that those forms having characteristics most nearly similar to the various short-tongued families of bees and to wasps were the most primitive. On the basis of this assumption, *Chelostoma* and *Prochelostoma* were considered to approach most nearly the primitive type because they have the longest parapsidal lines found in the Osmiini, an elongate thorax with the anterior part of the propodeum horizontal, and large pterostigmata. By contrast, *Osmia*, having punctiform parapsidal lines, is one of the most specialized genera of the group. Various other characters support this conclusion. *Diceratosmia* (a genus according to his classification) has the shortest parapsidal lines of all the more generalized genera and thus was placed immediately below *Osmia* in the phylogenetic tree. An examination has revealed extremely short parapsidal lines in *Osmia marginata* Michener, a desert species of *Nothosmia*. This species seems to be a connecting link between the generalized *Diceratosmia* and the slightly more specialized *Nothosmia*. All species of *Diceratosmia* possess a distinct carina along the inner ventral angle of each posterior coxa. Such a carina is represented in *marginata* and *O. (Chenosmia) caulicola* in the form of a weak line. This carina probably indicates primitiveness within the genus *Osmia*. It exists in stronger form in some of the most generalized genera of the *Osmiini* such as *Prochelostoma, Heriades, Noteriades,* and *Proteriades*. The

2. The name Osmiini is not used in recent classifications (Michener, 1944:256-268; Hurd and Michener, 1955:6-10) in which the groups are included in the tribe Megachilini. However, the name denotes a natural assemblage of nonparasitic megachilids having arolia.

TABLE I.—Primitive and Derived Characters in the genus *Osmia*.

Primitive	*Derived*
Size small	Size large
Pubescence white or pale, of moderate length	Pubescence dark or black, long or short
Mandible of female with three teeth	Mandible of female with four teeth
Mandible of male with upper tooth right angular or acute	Mandible of male with upper tooth obtuse
Mandibular constriction moderately wide	Mandibular constriction narrow, or absent and entire mandible broad
Mandible of female lacking transverse ridge or protuberance near base	Mandible of female having transverse basal ridge or protuberance
Malar space absent	Malar space present
Genal area of female lacking depression immediately below eye	Genal area of female with a round or elongate depression immediately below eye
Genal area of female equal to width of eye	Genal area of female significantly wider or narrower * than eye
Inner margins of eyes converging anteriorly	Inner margins of eyes parallel or diverging anteriorly
Clypeus of female lacking swollen or modified apical margin	Clypeus of female having apical margin swollen or otherwise modified
Clypeal punctations of female nearly confluent	Clypeal punctations of female widely separated or confluent
Clypeal margin of male having impunctate band of moderate width	Clypeal margin of male without or with narrow impunctate band
Hypostomal carina of female low	Hypostomal carina of female high, abruptly reduced behind angle, forming a tooth
Antennal socket having margin uniform throughout	Antennal socket having superior-mesal margin higher than remaining margin
Flagellar segments in male unmodified (cylindrical, about 1.5 times as long as wide)	Flagellar segments in male modified (moniliform, or last segment compressed and expanded, or each segment twice as long as wide)
Hind coxa with a ventral carina	Hind coxa without a ventral carina
Mediotarsal segments of middle leg of male not swollen	Mediotarsal segments of middle leg of male greatly swollen
Strigilis of male having malar spine not greatly produced	Strigilis of male having malar spine greatly produced
Basitarsus of hind leg of male lacking tooth	Basitarsus of hind leg of male having tooth on inner side
Forewing with hairs of cells short	Forewing with hairs of cells long
Middle femur of male lacking a projection on lower side	Middle femur of male having a projection on lower side
Hind basitarsus of male parallel-sided	Hind basitarsus of male modified (wider towards base, at apex, or in middle)
Metasomal terga with moderately wide impunctate bands	Metasomal terga without or with narrow or with wide impunctate bands
Metasomal sternum 2 of male lacking posterior tooth	Metasomal sternum 2 of male having posterior tooth

* Possibly the primitive condition.

TABLE 1.—Primitive and Derived Characters in the genus *Osmia* (CONCLUDED)

Primitive	*Derived*
Gonocoxite of male having weak subapical swelling	Gonocoxite of male lacking subapical swelling
Subapical hairs on gonocoxite of male diffuse	Subapical hairs on gonocoxite of male forming a tuft
Gonocoxite of male lacking a subapical process	Gonocoxite of male having a subapical process
Penis valve of male lacking long ventral longitudinal groove	Penis valve of male having long, ventral longitudinal groove

carina is absent in *Hoplitis,* but manifests itself in all forms of intergradation from a fairly conspicuous carina to a feeble line in the genus *Anthocopa,* which is comparatively less primitive in other characters than the previously mentioned genera. *O. (Diceratosmia) submicans* Morawitz (southern Europe, north Africa, etc.) strikingly resembles *O. (Nothosmia) marginata* from California in having extremely short parapsidal lines and weak or evanescent carinae on the hind coxae. *Diceratosmia* is judged to be the most generalized group of the genus *Osmia* and *Nothosmia* is a close relative which is also generalized and probably derived from the former early in the history of the genus.

In considering relations among subgenera, identical derived characters in some but not all species of each of two subgenera are regarded as an indication of probable relationship between the two subgenera concerned, except in instances where it is judged that there has been parallel evolution.

Diceratosmia retains twenty-eight of the twenty-nine primitive characters listed in Table 1. The only modification is the quadridentate condition of the mandible of the female. *Nothosmia* retains twenty-seven primitive characters and is specialized in two, namely, in having a tooth on the hind basitarsus in some males and in having the impunctate apical bands on the metasomal terga of the male narrow.[3] A common tendency towards mandibular constriction among the females of a few species of each subgenus supports the idea of close relationship of these two generalized subgenera.

The third most generalized subgenus is *Chenosmia;* it retains the same number of primitive characters as *Nothosmia,* but shares with *Diceratosmia* the derived quadridentate condition of the mandible in the female. The presence of a tooth on the hind basitarsus of the males in *Nothosmia* and the absence of such a tooth in some species of *Chenosmia,* together with the modification of the apical areas of

3. This and the following discussion suggests that there are few subgeneric characters. As the systematic section shows, there are some other characters which could not be included in Table 1 because of lack of information as to what alternatives are primitive.

the terga (impunctate bands narrow or absent) in *Nothosmia* suggest that *Chenosmia* did not arise from *Nothosmia*. *Chenosmia* probably arose from some *Diceratosmia*-like form near the point of divergence of *Nothosmia*.

The fourth generalized subgenus is *Euthosmia;* it retains twenty-five primitive characters of the twenty-nine listed in Table I and is specialized in four characters, namely, the sparseness of punctations on the clypeus of the female, greatly produced malar spine of the strigilis, modified hind basitarsus of the male, and absence of the carina on the hind coxa. In the first two characters, some species of *Diceratosmia* are likewise specialized. In the last two characters some species of *Nothosmia* are similarly specialized. These specializations bring *Euthosmia* equally close to *Diceratosmia* and to *Nothosmia*. *Euthosmia* was probably derived from *Diceratosmia* independently of other subgenera.

Acanthosmioides has twelve derived characters, and seems to have arisen from *Nothosmia* rather than from *Diceratosmia (Diceratosmia* differs from *Acanthosmioides* in thirteen characters) or *Chenosmia (Chenosmia* differs from *Acanthosmioides* in eleven characters). From *Nothosmia, Acanthosmioides* differs in only nine characters, and there are no modifications in *Nothosmia* that indicate that *Acanthosmioides* was not derived from that subgenus. Moreover, the tooth on the hind basitarsus of the male, which in itself is a significant modification for a generalized group like *Nothosmia*, occurs in *Acanthosmioides* as well.

Chalcosmia and *Centrosmia* have an equal number of primitive characters (see table II) and seem to be closely related to each other. Each has the same modifications, and in addition in some species of each subgenus the inner margins of the eyes diverge anteriorly. Because of these common characteristics, the two subgenera seem to be more closely related than either subgenus is to any other. *Centrosmia* is the more specialized of the two, as indicated by the modification of at least four structures (in some of its species) in which the species of *Chalcosmia* are primitive. Also, a few primitive characters of *Chalcosmia*, such as the abundance of pale-white or yellowish hairs on the body and the simple mediotarsal segments of the middle leg of the male, are probably qualitatively even more significant than the derived characters in relating the subgenus to the generalized subgenera, such as *Diceratosmia* and *Nothosmia*. *Centrosmia* and *Chalcosmia* have more characters in common than either has with *Nothosmia, Euthosmia* or *Chenosmia*. The generalized subgenus *Diceratosmia* could have given rise to

TABLE II.—Number of primitive and derived alternatives of twenty-nine characters among subgenera of *Osmia*

SUBGENUS	Alternatives		
	Primitive	Partly derived*	Derived
Diceratosmia	22	6	1
Nothosmia	21	6	2
Chenosmia	23	4	2
Euthosmia	24	1	4
Chalcosmia	17	2	10
Centrosmia	11	8	10
Acanthosmioides	13	4	12
Monilosmia	16	6	7
Cephalosmia	13	7	9
Trichinosmia	18	0	11
Osmia s. str.	13	4	12

* Partly derived means specialized in some species, not in others.

Chalcosmia. However, the narrowness or absence of the apical impunctate bands on the metasomal terga of *Nothosmia* is a modification not present in *Chalcosmia.* Modification of structures in *Euthosmia* indicate that it was not ancestral to *Chalcosmia* although the presence of well-separated punctations on the clypeus of the female of *Chalcosmia* is a modification suggesting *Euthosmia.* Therefore, it is logical to suppose that the common ancestor of *Chalcosmia* and *Centrosmia* arose from *Diceratosmia* (or the *Diceratosmia* stock) somewhere near the point of divergence of *Euthosmia* from the *Diceratosmia* stock. This ancestral line, in turn, split into *Chalcosmia* and *Centrosmia.*

In all of its derived characters (*e. g.,* the abundance of black pubescence on the body, the quadridentate mandible of the female, and the absence of a carina on each posterior hind coxa), the subgenus *Chenosmia* closely resembles the more specialized subgenus *Monilosmia.* The direction of specialization of some species of *Chenosmia,* such as from small to large size and from low to high hypostomal carinae in the female, indicates possible relations of *Chenosmia* to *Monilosmia,* in which these characters are strongly developed. Moreover, *Monilosmia* shares sixteen primitive characters with *Chenosmia,* thirteen with *Nothosmia* and only twelve with *Diceratosmia. Monilosmia* shares no derived character (in all its species) with *Diceratosmia* or with *Nothosmia.* The closeness of the relationship between *Monilosmia* and *Chenosmia* is further attested by the males of those two subgenera being almost indistinguishable. It is concluded that *Monilosmia* arose from

Chenosmia which, as previously stated, probably arose from the *Diceratosmia* line early in its history.

The subgenus *Osmia s. str.* preserves the minimum number of primitive characters. The absence of a tooth on the hind basitarsus of the male in *Osmia* is a primitive condition whereas *Nothosmia* is modified in this respect. At least some species of *Diceratosmia* and *Chenosmia* have this modification. The directions of modification within the subgenus are unexpected if judged by the characters of *Nothosmia, Diceratosmia, Chenosmia* or *Euthosmia.* Certain modifications (already discussed) of each of the other subgenera, except *Diceratosmia* and *Chenosmia,* similarly seem to prevent any one of them being considered as ancestral stock for the subgenus *Osmia.* It resembles *Chenosmia* in dark hair on the body, black scopa in the female and the quadridentate mandibles of the female (the latter condition is a modification also in the female of *Diceratosmia*). The broadened apical impunctate band on the clypeus of the male in some species of both *Chenosmia* and *Osmia s. str.* also suggests a possible relationship between these two subgenera. It is impossible to judge from these facts which, if any, of the generalized subgenera is directly ancestral to the subgenus *Osmia.* In addition, it was found impossible adequately to compare the subgenus *Osmia* with certain of other more specialized subgenera, namely *Centrosmia, Cephalosmia* and *Acanthosmioides,* because it was not possible logically to assume that any one of the three is either more generalized or more specialized than the subgenus *Osmia.* All that can be said is that *Osmia* possibly arose from *Diceratosmia* or *Chenosmia* somewhere near the point of divergence of these two subgenera. More probably the subgenus *Osmia* arose from an extinct ancestor of *Diceratosmia* and *Chenosmia.*

Trichinosmia is another subgenus of uncertain taxonomic position. With *Chenosmia, Trichinosmia* shares two modifications and with *Nothosmia* one. *Trichinosmia* is monotypic, and therefore, it cannot have some species with derived characters and some species with primitive characters. As in *Osmia s. str.,* the modifications seem to indicate relation to either *Diceratosmia* or *Chenosmia* instead of to any one of the specialized subgenera.

Cephalosmia preserved, among some species, more primitive characters than either *Chalcosmia* or *Centrosmia* (see table II) and shares more primitive characters with *Euthosmia* than with any other generalized subgenus. The derived characters so shared are the well-separated punctations on the clypeus of the female and the long malar spine of the strigilis of the male. *Cephalosmia* re-

sembles *Chenosmia* in fourteen characters of which two are derived (in which two derived characters *Cephalosmia* also resembles *Monilosmia*). Considering the characters in which only some species are specialized, *Cephalosmia* is equally related to *Chenosmia, Diceratosmia* and *Euthosmia.* But there is no modification in *Euthosmia* that indicates that *Cephalosmia* was not derived from that subgenus (such modifications occur in *Diceratosmia* and *Chenosmia*). Thus *Euthosmia* is perhaps ancestral to *Cephalosmia.*

Considering the problem of phylogeny, not from the standpoint of relative specialization but from that of intergradations between groups, we can note that *Diceratosmia* almost grades into *Nothosmia* and *Nothosmia* into *Acanthosmioides; Nothosmia* also almost grades into *Chenosmia* and *Chenosmia* into *Monilosmia* and *Monilosmia* into *Centrosmia.* Except for *Diceratosmia* this group of subgenera is almost exclusively American and it seems likely that *Trichinosmia* and *Euthosmia* and perhaps *Cephalosmia* are part of the same assemblage. The subgenera *Chalcosmia* and *Osmia s. str.* are more distinct, being separated by large gaps from each other and from any other subgenera. Both are primarily Eurasian with but few American species.

It will be noted that the most striking difference between the relationships indicated in the preceding paragraph and those outlined in earlier paragraphs concern *Centrosmia,* which was earlier associated with *Chalcosmia* and here with *Monilosmia.* It seems likely that the latter relationship is more correct.

PARALLELISMS

Numerous examples of parallel evolution have been observed in the independent acquisitions of similar characters among related subgenera. The most striking instances are:

1. The compressed last segment of the flagellum in the males of some species of *Acanthosmioides* and *Centrosmia.*
2. The thickened clypeal truncation in the females of *Centrosmia* and *Monilosmia* (some species).
3. The mesally directed, long and stiff hairs on the hypostomal area of the female in *Euthosmia* and *Monilosmia* (some species).
4. The sharp tooth near the angle of the hypostomal carina in the females of *Monilosmia, Chalcosmia,* etc.
5. The parallel or anteriorly diverging eyes in the females of some species of *Osmia, Cephalosmia, Acanthosmioides, Chalcosmia* and *Centrosmia.*

6. The absence or narrowness of the impunctate bands on the metasomal terga in the males of *Trichinosmia, Osmia, Nothosmia* and *Euthosmia* (some species).

7. The absence of the mid-apical emargination of the sixth metasomal tergum in the *Chalcosmia-Centrosmia* stock, in *Acanthosmioides* and in *Osmia.*

8. A subapical process on the gonocoxite of the males of *Acanthosmioides* (most species) and *Osmia* (one species).

Michener (1949c:140-141) has discussed the possible reasons for parallelisms in evolution; these reasons may apply equally well in the evolution of *Osmia.*

DISTRIBUTION

The genus *Osmia* is known from the Palearctic, Nearctic and Ethiopian regions. It is absent from the Indo-Australian and Neotropical regions. The subgenus *Diceratosmia* is known from southern Europe, Asia Minor, North Africa and probably ranges widely across Asia. In the New World this subgenus is widespread in the southern United States and extends southward to Costa Rica. This extensive distribution seems compatible with the generalized nature of the subgenus. *Diceratosmia* is found principally in the warmer parts of the north temperate regions. Hence it likely arose in such climates, perhaps when they extended into northern regions now much cooler. Perhaps it has been displaced from cooler climates by competition with more specialized subgenera, all of which are more boreal (except *Trichinosmia,* of which there is only one species). This is in agreement with Matthew's (1915) hypothesis that the most advanced groups (he was dealing mainly with higher taxa) should be nearest to the center of dispersal, and the most conservative groups farthest from it. Because the center of dispersal was assumed to be holoarctic, the generalized forms would be expected to be of southern occurrence now.

No species of *Nothosmia* is known from the Old World. In North America that subgenus occurs from coast to coast but not in cold, montane climates of the west. Species of group I of the subgenus are restricted to the eastern and central parts of North America. Species of group II occur in the desert areas from California to New Mexico. *Acanthosmioides,* a specialized subgenus probably derived from *Nothosmia,* is absent in the Old World and is restricted to mountainous and boreal regions of western North America. Females of *Acanthosmioides* closely resemble the species

group II of *Nothosmia*. White (1952) included five of the six species of group II of *Nothosmia* as an aberrant group of *Acanthosmioides*, not having seen the males of any of the species. In the New World, *Diceratosmia* probably gave rise to *Nothosmia* which in turn split into two groups; the predominantly eastern group I remained somewhat generalized whereas the western group II gave rise to the specialized subgenus *Acanthosmioides*. Perhaps group II of *Nothosmia* has become restricted to the southern deserts because that group could no longer survive elsewhere after the more specialized subgenera arose in country of the kind usually occupied by *Osmia*. This is in accordance with the view that, next to *Diceratosmia*, *Nothosmia* is the most generalized subgenus.

Chenosmia is distributed from coast to coast in North America but most of the species are in the mountains or boreal regions of the western half of the continent. *Monilosmia*, a closely related stock, is restricted to the western half of North America except for one species which ranges eastward to the Atlantic. The inclusion of *Osmia inermis* extends the known distribution of *Chenosmia* to Eurasia. Although there are many American species of *Chenosmia*, only this one Eurasian species is known to me; it is not especially generalized nor *Nothosmia*-like. It is a species of northern distribution and it is likely that it migrated to Eurasia from America during Pleistocene or post-Pleistocene time. *Monilosmia* is probably an independent group which arose from *Chenosmia* and remained restricted primarily to the mountainous regions of the western North America.

Chalcosmia is principally Eurasian, having many more species and more diversity there than in America; only one species group (plus one probably introduced European species) occurs in America. The comparatively more specialized subgenus *Centrosmia* is principally North American and probably originated in this continent, but one species, *O. nigriventris*, occurs in boreal parts of both America and Eurasia. Very likely it extended its range from America to Eurasia in Pleistocene or post-Pleistocene time.

Of the highly specialized subgenera, *Osmia* probably is of Old World origin as it has a larger number of species and exhibits more diversity there; only two species occur in North America. *Cephalosmia* is principally from high altitudes of the western half of North America and is unknown in the Old World. *Trichinosmia* is known from Arizona, Nevada and California in semideserts and in forested areas of low elevation.

FLOWER RELATIONSHIPS

In the literature and on the labels of specimens in collections, there are many records of flowers visited. Unfortunately most of these records do not distinguish between pollen collecting and nectar gathering visits, and therefore merely show that most species of *Osmia* can be collected from a wide variety of flowers. According to Michener (*in litt.*) females of *Chalcosmia* and *Cephalosmia* use pollen from Compositae in provisioning their nests. The remaining subgenera use pollen mostly from other families of plants. The subgenus *Osmia*, and perhaps *Nothosmia*, uses pollen from many families, perhaps with a preference for Leguminosae. Other subgenera utilize pollen principally from Scrophulariaceae, Leguminosae and Hydrophyllaceae. No American species of *Osmia* is known to be restricted in pollen collecting to one genus of plants.

OSMIA OF THE OLD WORLD

Ducke (1899:12-19) listed 266 species of the genus *Osmia* from Eurasia and Africa, and Friese (1911:35-160) lists 269 from the same continents. Numerous additional forms have been named since that time. Sandhouse (1939:1) and Michener (1951:1162-1172) recorded about 130 species from the Nearctic Region. This figure excludes the very numerous species of *Ashmeadiella*, *Proteriades*, *Anthocopa* and *Hoplitis* that would have been included in *Osmia* by European students of these bees. No systematic attempt has yet been made to correlate the fauna of the Old World with that of the New World with a view to presenting an all round picture of this large and widely distributed group. Michener (1941:147) has pointed out the complexity of the situation in a generic revision of the American Osmiinae, after studying about 60 Old World species, representing most of the named genera and subgenera. "In their treatment of the genera related to *Osmia*, European and American students have followed widely different paths. The European workers have placed the entire group in a single genus, *Osmia*, divided into a number of subgenera, some of which were unnatural, and to some of which untenable names were applied. American authors, on the other hand, following the example of Cresson, have usually recognized a considerable number of genera, especially among the forms related to Hoplitis." In his treatment, Michener followed a middle ground, not recognizing the fine divisions of Cresson at the generic level but dividing the unwieldy *Osmia* of European authors into a few major generic units.

Michener (1941:151), in considering the possible phylogenetic relationships, has recognized three major Old World genera, *Osmia*, *Anthocopa*, and *Hoplitis*, each with a number of subgenera. *Osmia* is the most distinct of the three genera and is easily recognized by the punctiform parapsidal lines. For reasons mentioned elsewhere in this paper, the previously recognized genus *Diceratosmia* is treated in the present study as a subgenus of the genus *Osmia* proper.

It is important to mention that a number of the Old World species of *Osmia* exist which cannot be satisfactorily classified under any of the three large genera recognized by Michener (1941:159). Perhaps some of these species have no close relatives in the New World and need to be grouped under separate genera, as suggested by Michener (1941:165) when he erected the genus *Stenosmia*.

In order to facilitate future work I have listed all the Old World species examined by me in three different groups below. Group I includes the species confined to the Old World which can be satisfactorily classified under genus *Osmia* in the sense of the present paper. Group II includes the species of *Osmia* which are common to both the New and the Old World. Group III includes the rest of the Old World species studied. Some are *Hoplitis*, some are *Anthocopa*, and some are questionable as to the genus to which they belong. Many of these species were placed by Michener (1941).

Group I: *Osmia aurulenta* (Panzer), *cornuta* Latreille, *decemsignata* (Radoszkowski), *dimidiata* Morawitz, *emarginata* Lepeletier, *fulviventris* (Panzer), *gallarum* Spinola, *kohlii* Ducke, *latreillei* Spinola, *leaiana* Kirby, *leucogastra* Morawitz, *longicornis* Morawitz, *medanae* Magretti, *notata* (Fabricius), *rubicola* Friese, *rufa* Linnaeus, *rufigastra* Lepeletier, *submicans* Morawitz, *taurus* Smith, *tricornis* Latreille, *versicolor* Latreille, *vidua* Gerstaecker.

Group II: *Osmia coerulescens* (Linnaeus), *inermis* (Zetterstedt), and *nigriventris* (Zetterstedt).

Group III: *Osmia adunca* (Panzer), *anthrenoides* Spinola, *atrocaerulea* Schilling, *balearica* Schmiedeknecht, *balucha* Nurse, *bicolor* (Schrank), *bidendata* Morawitz, *calviniae* Cockerell, *cephalotes* Morawitz, *claviventris* Thomson, *crenulata* Morawitz, *croatica* Friese, *difformis* Pérez, *ferruginea* Latreille, *flavicornis* Morawitz, *glutinosa* Giraud, *gracilicornis* Pérez, *jacoti* Cockerell, *jheringii* Ducke, *leucomelaena* (Kirby), *lhotellreici* Pérez, *ligurica* Morawitz, *macroglossa* Gerstaecker, *maritima* Friese, *mitis* Nylander, *moniliferum* Cockerell, *morawitzii* Gerstaecker, *panzeri* Morawitz, *papa-*

veris (Latreille), *paradoxa* Friese, *parvula* Dufour and Perris, *pilicornis* Smith, *quadridentata* Pérez, *ruficollis* Dours, *rufohirta* Latreille, *saundersii* Vachal, *scutellaris* Morawitz, *singularis* Morawitz, *spinolae* Schenck, *spinulosa* (Kirby), *transcaspica* Morawitz, *tridentata* Dufour and Perris, *tuberculata* Nylander, *uncinata* Gerstaecker, and *villosa* Schenck.

SYSTEMATIC TREATMENT

The genus can be recognized by the following characters: Body robust, coloration metallic blue to metallic green (dull and nonmetallic in a few species). Parapsidal lines reduced, punctiform or very short, each represented by a small, shining, often elevated area, sometimes no larger than one or two punctures, sometimes no more conspicuous than other unusually large interspaces between punctures, although usually definitely different from, and larger than, the latter; metanotum and the propodeum vertical or nearly so, propodeum without horizontal basal zone. First metasomal tergum with anterior face broadly concave, with a distinct line or carina separating this concavity from dorsal surface of tergum; male with seven exposed metasomal terga and tergum six not dentate laterally.

KEY TO THE SUBGENERA OF OSMIA IN AMERICA

Since several of the subgenera are most strikingly different from their relatives because of combinations of male and female characteristics, difficulties will be found in using the following key in which the sexes are separated. Most of the difficulties are indicated by qualifying words or by mention of exceptions, but caution must be used in placing a species, especially if it is available in only one sex.

Males

1. Posterior coxa having a distinct carina on inner ventral angle; mesoscutum with parapsidal line short linear, not punctiform, *Diceratosmia*

   Posterior coxa lacking a distinct carina on inner ventral angle; mesoscutum with parapsidal line punctiform or nearly so 2

2. (1) Metasomal sternum 2 with apical margin truncate or subtruncate, so that median length is not much greater than length measured laterally 3

   Metasomal sternum 2 with apical margin convex, largely covering sternum 3; median length greater than length measured laterally 4

3. (2) Genal area wider than greatest width of eye; pubescence white and black intermixed; hypostomal carina high; antennal socket with upper mesal margin more strongly developed than rest of margin ..... *Cephalosmia*

Genal area narrower than greatest width of eye; pubescence white; hypostomal carina low; antennal socket with margin uniformly developed throughout ..... *Euthosmia*

4. (2) Malar space distinct; middle leg having tarsal segments not swollen, middle femur having weak or strong projection on lower surface ..... *Osmia s. str.*

Malar space absent or narrow, wide only in *bucephala;* middle leg having tarsal segments swollen or not; middle femur lacking projection on lower margin 5

5. (4) Metasomal sternum 4 with apical margin thickened, transversely sulcate in lateral portions. Metasomal terga 1 to 5 each having a subapical band of plumose hair ..... *Chalcosmia*

Metasomal sternum 4 with apical margin not modified as above. Metasomal terga 1 to 5 lacking distinct subapical bands of plumose hair 6

6. (5) Middle leg with tarsal segments 2 and 3 greatly swollen (except in *bakeri* and *nigriventris*); metasomal tergum 6 without or with very faint and undefined emargination (except in *nigriventris* which is black); flagellar segment 11 unmodified (except in *vandykei* which has a median basal tuft of long hairs on metasomal tergum 6) ..... *Centrosmia*

Middle leg with tarsal segments 2 and 3 not swollen; if swollen, antennal segments modified; metasomal tergum 6 having shallow or deep midapical emargination, usually delimited by distinct angles 7

7. (6) Metasomal sternum 2 with protuberance or tooth on median apical or subapical area (except in *O. integra* which has median band of unusually long hair on this sternum); hind basitarsus usually narrow basally and widened distally, *Acanthosmioides*

Metasomal sternum 2 lacking protuberance or tooth on median apical or subapical area; hind basitarsus variable 8

8. (7) Impunctate bands on terga 1 to 3 narrow or absent, usually not depressed (distinct and depressed in certain eastern species of *Nothosmia*); pubescence usually entirely white 9

Impunctate bands on terga 1 to 3 wide and distinct, depressed (in *seclusa,* bands punctate but broadly depressed); pubescence often partially black 10

9. (8) Flagellar segments 2 to 11 each twice as long as wide; forewing with hairs about half as long as width of pterostigma; hind basitarsus lacking a tooth; metasomal terga 2 to 5 with hairs simple, erect; head and thorax with long-branched hairs, *Trichinosmia*

Flagellar segments 2 to 11 less than twice as long as wide; forewings with hairs much less than half as long as width of

pterostigma; hind basitarsus with a tooth; metasomal terga 2 to 5 with some plumose hairs and usually with apressed hairs at least near posterior margins of terga; head and thorax with short-branched hairs ..... *Nothosmia*

10. (8) Metasomal tergum 7 with deep midapical emargination; strigilis with malar spine long; hind leg with tibial spurs curved apically; size usually about 10 mm.; color dark blue, often having greenish tinge ..... *Monilosmia*

Metasomal tergum 7 with shallow midapical emargination; strigilis with malar spine short; hind leg with tibial spurs not curved or weakly curved apically; size usually less than 10 mm.; color metallic green or dark green ..... *Chenosmia*

Females

1. Posterior leg having a distinct carina on inner ventral angle of each hind coxa; mesoscutum with parapsidal line short linear, not punctiform ..... *Diceratosmia*

Posterior leg lacking distinct carina on inner ventral angle of each hind coxa; mesascutum with parapsidal line punctiform, 2

2. (1) Mandible having four distinct teeth (three in *zephyros;* second tooth much reduced in *cerasi*) 3

Mandible three-toothed, having first, third, and fourth teeth, or, if a small second tooth is present, either the pubescence is all white or the mandible is slender medially, two-thirds or one-half apical width 9

3. (2) Malar space wide; a round or elongate depression in genal area immediately below lower posterior angle of eye ..... *Osmia s. str.*

Malar space in most species narrow or absent, or if wide, having clypeal margin greatly swollen; depression in genal area immediately below lower posterior angle of eye absent 4

4. (3) Clypeal truncation tridentate with one median and two lateral teeth; hair on head and thorax with long branches; hairs on forewing long, two-thirds as long as width of pterostigma, *Trichinosmia*

Clypeal truncation usually simple, if modified, not as above; hair on head and thorax with short branches; hairs on forewing short, less than half as long as width of pterostigma, dense or sparse 5

5. (4) Clypeus with punctations separated by smooth ground or sometimes largely absent; antennal socket with upper mesal margin more strongly developed than rest of margin; metasomal tergum 6 with apical margin not produced to form a flange (except in *californica*) ..... *Cephalosmia*

Clypeus with punctations confluent at least on anterior half; antennal socket with margin uniformly developed; metasomal tergum 6 with apical margin produced forming a flange 6

6. (5) Mandible with protuberance or transverse ridge on outer surface near base; clypeus with apical margin thickened or with two median sockets just beneath margin and mesal to usual hair tufts, each giving rise to a tuft of hairs 7

Mandible without transverse ridge or protuberance near base except in *seclusa* and *rostrata* which have a ridge; clypeus with apical margin not thickened (except in *rostrata*) nor with two median sockets each giving rise to a tuft of hairs 8

7. (6) Clypeal margin with two small median sockets each giving rise to a small tuft of hairs in addition to two large lateral tufts; metasomal terga 2 to 5 each with a subapical band of plumose hairs, without apical impunctate band ..... *Chalcasmia*

Clypeal margin swollen, without two median sockets each giving rise to a tuft of hair in addition to two large lateral tufts; metasomal terga 2 to 5 without subapical bands of plumose hairs, with apical impunctate bands ..... *Centrosmia*

8. (6) Hypostomal carina high, abruptly reduced near angle, forming a tooth; genal area wider than eye; clypeal truncation usually longer than margin from end of truncation to lateral angle of clypeus ..... *Monilosmia*

Hypostomal carina low, not abruptly reduced near angle; genal area as wide as eye; clypeal truncation usually equal to margin from end of truncation to lateral angle of clypeus *Chenosmia*

9. (2) Tufts of orange hairs beneath clypeal margin absent; strigilis with inner concavity of velum deep, malar spine slender, acuminate; scopal hairs restricted to a subapical band, half as wide as distance from gradulus to sternal margin, on each sternum, *Euthosmia*

Two tufts of orange hairs beneath clypeal margin; strigilis with inner concavity of velum shallow, malar spine greatly widened at base; scopal hairs not restricted to a subapical band on each sternum 10

10. (9) Scopa white to testaceous (black and white intermixed in *marginata*, black in *liogastra*); metasomal terga 1 to 3 each with or without a narrow apical impunctate band ..... *Nothosmia*

Scopa black; metasomal terga 1 to 3 each with wide apical impunctate band (except *sedula* which has much darker body with more black hairs than *Nothosmia*) ..... *Acanthosmioides*

Subgenus *Diceratosmia* Robertson

Diceratosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 166, 171; Cockerell, 1912, Proc. U. S. Nat. Mus., vol. 42, p. 216; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 1; Michener, 1941, Amer. Midland Nat., vol. 26, p. 162; Michener, 1949, Ann. Ent. Soc. Amer., vol. 42, pp. 258. *Type species*: *Osmia quadridentata* Cresson, 1878 (not *Phyllotoma quadridentata* Duméril) = *Osmia conjuncta* Cresson, 1874, original designation.

This subgenus can be distinguished from all others by the longitudinal carina along the inner ventral angle of each posterior coxa and by the slightly elongate parapsidal lines of the mesoscutum. These characters are, as indicated elsewhere, weakly developed in an occasional *Nothosmia*.

Male. — Length of body 6 to 10 mm. Pubescence white; metasomal terga with subapical fasciae. *Punctation on general body*

surface coarse in most American forms. Mandible widest at base, narrower at region of constriction which is nearly as wide as apex, with V-shaped notch separating lower tooth from subtruncate to oblique, acute upper tooth; eye wider than genal area; inner margins of eyes parallel or weakly converging anteriorly; clypeus thickly covered with white hairs arising from coarse and confluent punctures, apex weakly wavy, arcuately emarginate, or with median third projecting, with narrow or moderately wide impunctate apical band; scape longer than second to fourth antennal segments combined; flagellar segments 2 to 11 unmodified, each less than twice as long as wide; hypostomal carina low, uniform throughout. Middle leg with tarsal segments not swollen; *parapsidal lines short linear; posterior coxa with carina along inner ventral angle;* basitarsus of hind leg about five times as long as wide, not toothed, parallel sided; strigilis with apical margin of velum truncate or obliquely truncate, inner apical angle of velum narrowly rounded, concavity on inner margin of velum shallow, apex of malus produced into a long and moderately narrow spine. Forewing cells with short, moderately sparse hair, distal portion finely papillate. Metasomal terga 2 to 5 without impunctate bands (except narrow bands on posterior terga of *conjuncta*); apical margin of tergum 6 with greatly widened emargination, median third of base of emargination produced, with or without emargination or subtruncation at apex of production, lateral portion turned up, forming a flange; tergum 7 with apex produced, midapex with a deep emargination, forming two lobes or teeth. Metasomal sternum 1 broadly rounded with shallow midapical emargination; sternum 2 with apical margin produced and broadly rounded, covering most of sternum 3, apex subtruncate or with a shallow emargination; sternum 3 with a wide, deep emargination; sternum 4 with apical margin broadly convex; sternum 6 with a median apical produced portion the apex of which has a shallow, wide emargination; sternum 8 with apical half broadly convex or narrowly triangular. Gonocoxite broad subapically, abruptly narrowed to a short process.

Female.—Length of body 7.5 to 12 mm. Pubescence long or short, branching of hair close and short, white or reddish brown; metasomal terga with subapical fasciae; scopa white or brownish. Mandible moderately broad, constricted distad of base, gradually widened to apex, which is oblique and a little less than twice as wide as constriction, lacking transverse ridge or protuberance at base, with three or four teeth, third and fourth teeth triangular;

distance between teeth 1 and 3 equal to or longer than that between teeth 3 and 4; eye about as wide as genal area; inner margins of eyes parallel to slightly converging below clypeus with punctures confluent (separate on sides in *azteca*), median half or two-thirds of truncation produced, apex of projection truncate, apex of truncation longer than margin from end of truncation to lateral angle of clypeus; hypostomal carina not greatly produced, highest immediately behind angle. *Parapsidal lines short linear; posterior coxa with carina along inner ventral angle;* hind leg with basitarsus about four times as long as wide, widest near base and gradually narrowed toward apex, which is subtruncate or rounded; hind tibial spurs straight to weakly curved. In forewing, cells with short (long in some areas), moderately sparse hairs, distal part with fine and dense papillae. Metasomal terga 2 to 5 lacking apical impunctate bands; tergum 6 with apical margin forming a flange.

New World species included: *Osmia* (*Diceratosmia*) *azteca* Cresson, *botitena* Cockerell, *conjuncta* Cresson, *subfasciata* Cresson.

The Old World species included: *Osmia* (*Diceratosmia*) *gallarum* Spinalo, *rufigastra* Lepeletier, *submicans* Morawitz, and *versicolor* Latreille.

Species of *Diceratosmia* are widespread in the Old World; in the New World they range across the southern United States and extend southward to Costa Rica. The American species of the subgenus were revised by Michener (1949b).

The above description is based on New World forms.

Subgenus *Nothosmia* Ashmead

Nothosmia Ashmead, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 75; Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 63. *Type species: Osmia distincta* Cresson, 1864, original designation and monobasic

Leucosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 166, 171. *Type species: Osmia albiventris* Cresson, 1864, original designation and monobasic.

Xanthosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 166, 171. *Type species*: *Osmia cordata* Robertson, 1902, original designation and monobasic.

Nothosmia can be recognized by the complete absence of black hairs in both sexes (except in a few desert species), by the absence or narrowness of apical impunctate bands of the metasomal terga, by vein A being at least twice the length of vein B in forewing of the male, by presence of a tooth on the anterior margin of the hind basitarsus of the male and by the subequal lengths of the clypeal truncation and the margin from the end of the truncation to the lateral angles of clypeus in female.

Male.—Length of body 6 to 9 mm. Pubescense white (partially black in *prunorum*); metasomal terga often without apical or subapical fasciae. Mandible slender, widest at base, narrowed distad of base in some species, gradually widened to apex which is often less than twice as wide as constriction. Genal area as wide as or narrower than eye; inner margins of eyes converging anteriorly; clypeus densely covered with white hairs (most dense in *titusi* and *prunorum*) arising from fine (finest in *titusi*) and confluent punctures, apical margin crenulate, subtruncate or slightly concave, with moderately wide impunctate apical band; scape equal to or slightly longer than second to fourth antennal segments combined; flagellar segments 2 to 11 unmodified, each less than twice as long as wide; hypostomal carina usually low and uniform, in some species gradually raised from posterior end to angle, but never greatly produced. Middle leg with tarsal segments not swollen; hind basitarsus three and one-half to five times as long as wide, toothed, widest at apex, gradually narrowed toward base; strigilis with apical margin of velum truncate, inner apical angle of velum narrowly subtriangular, concavity of inner margin of velum shallow to moderately deep, apex of malus usually produced into a long pointed spine. Forewing cells usually with dense, short, hairs (except scattered long hairs in *inspergens*), apical part papillate, vein A twice as long as vein B. Metasomal terga 2 and 3 with apical impunctate band narrow or absent, that of 4 and 5 sometimes wider; midapex of tergum 6 with a shallow or deep emargination; tergum 7 with apex produced, midapex of projection emarginate forming two sharp teeth. Metasomal sterna 1 and 2 with apical margins broadly rounded, sternum 2 without ventral midapical projection; sternum 3 with shallow or deep median apical emargination which is thickly fringed with long hair or short hairs; sternum 4 with apical margin subtruncate or broadly rounded; sternum 6 with apex broadly rounded or subtruncate medially; sternum 8 with basal half narrowly triangular, apical half broadly subtriangular, with apex subtruncate, rounded or with a low median projection. Gonocoxite without any process arising before apex, swollen at angulation which bears tuft of bristles.

Female.—Length of body 8 to 11 mm. Pubescense not loosely branched, white (partially black in *marginata* and *liogastra*); metasomal terga without apical or subapical fasciae (except in *pumila, titusi* and *marginata*); color of scopa white to yellowish (black in *liogastra,* black and white mixed in *marginata*). Mandible slender, constricted moderately or strongly distad of base, gradually wid-

ened to apex which is slightly oblique, little wider than to twice as wide as width of constriction, base without transverse ridge or protuberance, apex tridentate, second tooth if present, rudimentary or continuous with first, third and fourth teeth narrowly triangular, distance between teeth 1 and 3 equal to or longer than distance between teeth 3 and 4; genal area narrower than or subequal to eye width; inner margins of eyes converging anteriorly; clypeal truncation simple or with a wide midapical projection, apex of which is truncate, truncation subequal to or shorter than margin from end of truncation to lateral angles of clypeus; hypostomal carina not greatly produced, usually higher than in males, uniform throughout posterior part, slightly higher than anterior part. Hind basitarsus three to four times as long as wide, of uniform width throughout, or slightly wider near base than elsewhere, apex rounded; hind tibial spurs moderately curved apically or almost straight. Forewing moderately to extremely hyaline, hairs in cells short, dense (*cordata* with longer and sparse hairs), apex papillate. Metasomal terga 2 to 5 with or without narrow impunctate apical bands; tergum 6 with apical margin forming a flange.

Species included: *Osmia (Nothosmia) albiventris* Cresson, *cordata* Robertson, *distincta* Cresson, *inspergens* Lovell and Cockerell, *liogastra* Cockerell, *lupinicola* Cockerell, *marginata* Michener, *morongana* Cockerell, *prunorum* Cockerell, *pumila* Cresson, *sandhouseae* Mitchell, *titusi* Cockerell.

The subgenus is here divided into two groups, I (restricted to the eastern half of the United States and Canada) and II (found in the southwestern deserts) in order to show the characteristics of each group of species.

Group I (*albiventris, cordata, distincta, inspergens, pumila* and *sandhouseae*): These species can be recognized by the following characteristics: In the female there is usually a small, sometimes weak, concavity at each end of the clypeal truncation; each mandible has four teeth; the apices of the mandibles are much less than twice the widths at the constrictions; the eyes are subequal to or slightly narrower than the genal areas; and the scopa is white. In the male the color of the antennae and tegulae is brown, darker than that of group II; the wings are less hyaline than those of group II; and the metasomal terga usually lack subapical fasciae of simple or plumose hair.

Group II (*liogastra, lupinicola, marginata, morongana, prunorum,* and *titusi*): These species can be distinguished by the following characteristics: In the female the apical margin of the clypeus

lacks a concavity at each end of the truncation; the mandibles are tridentate, constricted medially, the apices twice the widths at the constrictions or nearly so; the eyes are wider than the genal areas (subequal in *titusi* and *prunorum*); and the color of scopa varies from white, white mixed with black, to black. In the male, the antennae (ventral and lateral aspects only in some) and tegulae are testaceous; the wings are extremely hyaline; and the metasomal terga are provided with weak subapical fasciae of simple hairs. Most of the species of this group were treated by White (1952), who included them in *Acanthosmioides.*

Chenosmia, new subgenus

Type species: *Osmia pentstemonis* Cockerell, 1906.

This is the largest North American subgenus of *Osmia.* Females can be distinguished from those of the closely related subgenus *Monilosmia* by the equal widths of the eyes and genal areas, the equal lengths of clypeal truncation and the margin from the end of the truncation to the lateral angle of the clypeus, and the low hypostomal carinae that are not abruptly reduced and hence not toothed near the angles. Distinctive recognition characters in males are few. Males usually differ from those of *Monilosmia* in the shorter malar spine of the strigilis, the straight or weakly curved hind tibial spurs, the shallow emargination of metasomal tergum 7, and the toothed basitarsi in a large number of species.

Male.—Length of body 5 to 11 mm., usually less than 10 mm. Color of body in some species bright metallic green or blue; when of a dull metallic color, it is commonly green; metallic coloration lacking in *inermis.* Pubescence white with black intermixed in some areas; metasomal terga (except tergum 1) in most species without apical or subapical fasciae. Mandible slender or moderately wide, widest at base, narrower at region of constriction which is subequal to or slightly wider than apex, with V-shaped notch separating lower tooth from truncate or oblique, acute to right-angled upper tooth; width of genal area less than eye; inner margins of eyes distinctly converging anteriorly; clypeus with apical margin weakly wavy to serrate, often weakly emarginate, moderately to broadly impunctate; scape subequal to second to fourth antennal segments combined; flagellar segments 2 to 11 less than twice as long as wide; hypostomal carina not greatly produced, usually uniformly low. Middle leg with tarsal segments not swollen; hind basitarsus three to four times as long as wide, parallel sided or narrower basally and gradually widened towards apex, often with

a small tooth on inner margin; strigilis with inner apical angle of velum rounded, apex of velum truncate or subtruncate; apex of malus produced into short spine; emargination of inner margin of velum shallow to moderately deep. Forewing cells usually with dense and short hairs, distal part with short papillae, vein A usually less than twice as long as B (more than twice in *collinsiae, indeprensa, nanula,* and *proxima*). Metasomal terga 2 to 5 with broad apical impunctate bands (narrow on terga 2 and 3 in *collinsiae*); tergum 6 with apical emargination which is usually shallower than in subgenus *Monilosmia;* tergum 7 with apex produced, midapex of projection emarginate, usually forming two teeth. Metasomal sternum 1 with apex broadly convex, often with shallow midapical emargination; sternum 2 large, without apical process or tooth, covering most of third; distal portion of second strongly produced, apex convex, sometimes subtruncate medially or with shallow midapical emargination; median apical third of sternum 3 with an emargination which is fringed with long hairs; sternum 4 with apical margin convex, or middle third to half weakly to strongly produced, subtruncate to truncate; sternum 6 with a low, wide, rounded median projection, tip of which may be truncate or emarginate; sternum 8 with apical half more broadly triangular than basal half, tip occasionally produced. Gonocoxite simple without a process arising before apex, tapering from base to short distance beyond tip of volsella, then weakly to strongly swollen and angulate, beyond angulation tapering to apex.

Female.—Length of body 8 to 14 mm., usually less than 10 mm. Pubescence short and not loosely branched, metasomal terga without subapical or apical fasciae; hairs white mixed with black, sometimes largely black. Mandible not broad, slightly constricted distad of base, gradually widened to apex which is much less than twice as wide as width of constriction, lacking transverse ridge or protuberance near base, with four teeth (three in *cerasi* and *zephyros*), teeth narrowly to broadly triangular, second tooth often almost continuous with and subequal to first; distance between teeth one and three more than distance between three and four (except in *cerasi* and *zephyros*); genal area as wide as eye (slightly wider in *dolerosa, malina,* and *robustella*); inner margins of eyes slightly to distinctly converging; clypeus with punctures confluent, truncation not swollen (except in *indeprensa*), usually equal to margin from end of truncation to lateral angle of clypeus; malar space absent; hypostomal carina low and uniform, often slightly raised behind angle, any resulting tooth low and rounded. Hind

basitarsus three to nearly four times as long as wide, usually widest in middle, gradually tapering towards base and apex, apex truncate to subtruncate; hind tibial spurs distinctly curved at tips. Forewing with hairs on cells usually dense and short (sparse and longer in *bruneri*, *cerasi*, and *cyanopoda*). Metasomal terga 2 to 5 with apical impunctate bands narrow to broad; tergum 6 with apical margin forming a flange.

North American species included in this subgenus: *Osmia* (*Chenosmia*) *atriventris* Cresson, *bruneri* Cockerell, *calla* Cockerell, *caulicola* Cockerell, *cerasi* Cockerell, *clarescens* Cockerell, *cobaltina* Cresson, *collinsiae* Robertson, *cyanopoda* Cockerell, *dolerosa* Sandhouse, *exiqua* Cresson, *illinoensis* Robertson, *indeprensa* Sandhouse, *inermis* (Zetterstedt), *kincaidii* Cockerell, *laeta* Sandhouse, *malina* Cockerell, *nanula* Cockerell, *pentstemonis* Cockerell, *pingreeana* Michener, *pagosa* Sandhouse, *potentillae* Michener, *proxima* Cresson, *regulina* Cockerell, *sanctae-rosae* Cockerell, *sequoiae* Michener, *tersula* Cockerell, *tokopahensis* Michener, *trevoris* Cockerell, *tristella* Cockerell, *zephyros* Sandhouse.

This subgenus is represented in the Old World so far as known by only one species, *Osmia (Chenosmia) inermis* (Zetterstedt), which also occurs in boreal North America.

Euthosmia, new subgenus

Type species: Heriades glaucum Fowler, 1899.

Sandhouse (1939:64) included all the species of *Euthosmia* under the subgenus *Nothosmia*, but they seem different enough to be recognized as the members of a distinct subgenus. A combination of the following characters separates this group from all other subgenera of *Osmia*. In the male the apical margin of the second sternum is subtruncate and does not overlap the third to any extent; the apical margin of sternum 3 is without or with only a shallow median emargination; the apical margin of sternum 6 is broadly subtriangular; the basal half of sternum 8 is narrowly triangular and the distal half bears a median projection (subtriangular in *claremontensis*); the apex of the velum is truncate; the spine of the malus is slender and usually long; and the inner margin of the velum is deeply emarginate. In the female the bases of the maxillary stipites and also the ventral area of the head have long curled hairs; the scopa is pale; the tridentate mandible is slightly narrower at the constriction than at the apex; the strigilis has a long sharp apical malar spine projecting downward, the apex of the velum is truncate and the inner margin of the velum deeply emarginate.

Because no females of *nemoris* and *claremontensis* have been described, the female characters cited here are of *glauca* only.

Male.—Length of body 4 to 11 mm. Pubescence white. Mandible slender, widest at base, constricted just distad of base, lateral margins from constriction to apex subparallel, with V-shaped notch separating long slender lower tooth from truncate or oblique upper tooth; eye wider than genal area, inner margins of eyes distinctly converging anteriorly; clypeus covered with erect, white hairs arising from fine contiguous punctures, apex truncate, weakly wavy to crenulate with narrow to moderately wide impunctate apical band; scape subequal to or slightly shorter than second to fourth antennal segments combined; flagellar segments 2 to 11 each less than twice as long as wide (in *glauca*, nearly twice as long as wide); hypostomal carina low and of uniform height anterior and posterior to angle. Second and third tarsal segments of middle leg not swollen; hind basitarsus three to four times as long as wide, not toothed, of uniform width throughout or gradually widened towards apex; strigilis with apical margin of velum truncate, inner apical and basal angles acute, pointed; concavity at inner margin of velum deep; spine of malus long (short in *claremontensis*). Forewing with vein A twice to less than twice as long as vein B; papillae on distal part fine, dense; hairs on cells short, dense. Metasomal terga 2 to 5 with moderate to broad impunctate bands, with subapical fasciae of hairs (except in *glauca*); apical margin of tergum 6 with or without shallow poorly defined emargination at midapex; apex of tergum 7 produced, midapex of projection emarginate, forming two, usually sharp teeth. Metasomal sterna 2 and 3 with apical margins truncate to weakly convex; sternum 4 weakly to strongly convex; sternum 5 broadly rounded with or without shallow median emargination; sternum 6 with apical margin broadly subtriangular; sternum 8 with basal half triangular and base strongly acuminate, distal half with median projection (more broadly triangular in *claremontensis*). Gonocoxite tapering slightly from base to angulation (strongly angulate in *claremontensis*).

Female.—Length of body 6 to 8 mm. Scopa white. Metasomal terga without apical or subapical fasciae. Mandible wide, slightly constricted distad of base, gradually widened to apex, which is a little wider than at constriction; protuberance or transverse ridge near base of mandible absent; apex tridentate with teeth blunt, short, two upper teeth almost continuous, lower tooth triangular; distance between teeth one and three slightly longer than between three and four; width of genal area subequal to width of eye; inner

margins of eyes converging anteriorly; clypeus with punctures separate, margin not swollen, apical truncation slightly longer than margin from end of truncation to lateral angle of clypeus; *tufts of orange hair, arising beneath clypeal margin absent.* Hypostomal carina uniform, slightly higher behind angle than anteriorly; *hypostomal area with medially directed long stiff bent hairs.* Basitarsus of hind leg over three times as long as wide, subparallel sided, apex rounded; hind tibial spurs almost straight at apices; strigilis with apical spine of malus longer than in male, inner margin of velum strongly emarginate. Forewing with hairs in cells fine, dense. Metasomal terga 2 to 5 with narrow apical impunctate band; tergum 6 with apical margin forming flange. Scopa restricted to apical halves of metasomal sterna 2 to 5.

Species included: *Osmia (Euthosmia) claremontensis* Michener, *glauca* (Fowler) and *nemoris* Sandhouse.

This subgenus is restricted to the Pacific Coast of North America. The possibility exists that *glauca* (= *exilis* Sandhouse) is not closely related to the other species; this is perhaps suggested by the medially produced sixth tergum of males of *claremontensis* and *nemoris.* Until females of these species are known, it will be difficult to decide this matter.

Subgenus *Acanthosmioides* Ashmead

Acanthosmioides Ashmead, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 76; Cockerell, 1912, Proc. U. S. Nat. Mus., vol. 42, p. 216; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 39; White, 1952, Univ. Kansas Science Bulletin, vol. 35, p. 219. *Type species: Osmia odontogaster* Cockerell, 1897, original designation and monobasic.

White (1952) revised the subgenus in detail and included twenty-five species. Five desert species (*liogastra, lupinicola, morongana, prunorum,* and *titusi*) grouped under the subgenus by White have been excluded in this revision and transferred to the subgenus *Nothosmia.* The main recognition characters of this subgenus are the constriction of the mandible distal to the base so that in the female the apex is about twice, and in the male at least one and one-half times, the width of the constriction. In females this character is shared by the western group of *Nothosmia.* In males, metasomal sternum 2 usually has a midapical tooth or projection and the gonocoxite is provided with a subapical process.

Male.—Length of body 8 to 14 mm. Pubescence white with black intermixed; metasomal terga without apical or subapical fasciae. Mandible slender, widest at apex which is at least one and one half times as wide as constriction; apex with V-shaped notch separating

long slender, lower tooth from truncate or oblique, obtuse or right angular upper tooth; eye slightly to moderately wider than genal area; inner margins of eyes subparallel to slightly converging; clypeus very thickly covered with erect, white hairs arising from extraordinarily fine and confluent punctures, apex produced, subtruncate with narrow, thickened, impunctate margin, median portion dentate; scape usually equal to antennal segments 2 to 4 combined; flagellar segments 2 to 11 each less than twice as long as wide, last segment sometimes compressed and expanded or flagellar segments moniliform; hypostomal carina not greatly produced, usually low and gradually raised from posterior end to angle. Middle leg with tarsal segments usually not swollen, but in *longula* mediotarsal segments of fore and middle legs much enlarged; hind basitarsus about three times as long as wide, not toothed, of uniform width or widened distally; strigilis with inner apical angle of velum rounded; apex of velum subtruncate; apex of malus produced into a short to slightly longer sharp spine; concavity on inner margin of velum usually deep. Forewing cells with short hairs, distal portion papillate, vein A usually twice as long as vein B. Metasomal terga 2 to 5 with wide apical impunctate bands, usually with subapical fimbriae of simple hairs; tergum 6 with apical margin with or without a weak and poorly defined apical emargination, forming two lobes or teeth. Metasomal sternum 1 with apical margin subtruncate, convex or narrowly subtriangular, with median emargination; sternum 2 large, largely covering third, ventral surface with a median apical projection or protuberance on each side of which the apical margin is fringed with long hairs (except *integra* which has no projection or protuberance, but has a median band of long hairs); sternum 3 with a shallow midapical emargination which is fringed with long hairs; sternum 4 with a median apical patch of hairs bent mesad at tips, surrounding an impunctate portion of varying shape; sternum 6 with a median apical produced portion with apex either truncate or slightly emarginate; sternum 8 much reduced with apical half either triangular or produced into a subtriangular process, basal half wide to middle, then abruptly narrowed to a slender tip (except *longula* where it is broadly subtriangular). Gonocoxite with a process arising before its apex, apical half of the process usually spatulate, distal portion of gonocoxite abruptly narrowed, slender and hairless.

Female.—Length of body, 8 to 15 mm. Pubescence usually not long and loosely branched, scopa black. Mandible slender, con-

stricted just distal to base, gradually widened to apex, which is usually twice as wide as width of constriction, lacking transverse ridge or protuberance near base, tridentate (rudiment of second tooth absent in most species); distance between teeth 1 and 3 equal to or slightly shorter than distance between 3 and 4; eye usually narrower than genal area but often subequal to it; inner margins of eyes slightly converging (parallel in *calcarata, integra,* and *longula*); clypeus with punctures confluent, with truncation unthickened, equal to or slightly shorter than distance from end of truncation to lateral angle of clypeus; hypostomal carina not much elevated, highest at or near angle, not forming tooth. Hind basitarsus a little wider just before base than elsewhere, apex subtruncate to rounded; hind tibial spurs relatively straight, rarely much curved at tips. Forewing hairs in cells short, dense, papillae on distal part sparse, dense in some areas. Metasomal terga 2 to 5 with moderately wide apical impunctate bands (scattered punctures extend to apical margins in *sedula*); tergum 6 with apex forming a strong flange.

Species included: *Osmia (Acanthosmioides) ashmeadii* (Titus), *calcarata* White, *dakotensis* Michener, *francisconis* White, *giliarum* Cockerell, *giffardi* Sandhouse, *hurdi* White, *integra* Cresson, *kenoyeri* Cockerell, *lanei* Sandhouse, *longula* Cresson, *nifoata* Cockerell, *nigrifrons* Cresson, *nigrobarbata* Cockerell, *obliqua* White, *odontogaster* Cockerell, *physariae* Cockerell, *sedula* Sandhouse, *sladeni* Sandhouse, *trifoliama* Sandhouse, *unca* Michener, *watsoni* Cockerell.

The species of this subgenus are restricted to western North America.

Subgenus *Monilosmia* Robertson

Monilosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 166, 171. *Type species: Osmia canadensis* Cresson, 1864 = *Osmia simillima* Smith, 1853, by original designation and monobasic.

This subgenus resembles *Chenosmia* in general characters but females of *Monilosmia* can be distinguished as follows: The clypeal truncation is longer than the distance from the end of the truncation to the lateral angle of the clypeus; the genal areas are wider than the eyes; the hypostomal carina is high, abruptly reduced near the angle, forming a tooth (often rounded). Species of this subgenus are larger than most *Chenosmia* (usually about 10 mm. long) and generally darker blue. In the male, there is no single diagnostic character for the subgenus which is applicable to all the species. Nevertheless a combination of larger size, the longer

malar spine of the strigilis, the curved apices of the tibial spurs, the deeper emargination of the seventh metasomal tergum, the absence of a tooth on the basitarsus of the hind leg, and the sparser hairs in the cells of forewing help to distinguish males of *Monilosmia*, in general, from those of *Chenosmia*.

Male.—Length of body 7 to 11 mm. Color of body dark blue to greenish blue. Pubescence black and white; metasomal terga (except tergum 1) without apical or subapical fasciae. Mandible widest at base, narrower at region of constriction which is slightly narrower to wider than apex, with V-shaped notch separating usually long lower tooth from acute to right angular upper tooth; eye equal to or wider than genal area; inner margins of eyes slightly to distinctly converging anteriorly; clypeal margin weakly wavy to strongly crenulate, narrowly or broadly impunctate; scape usually subequal or equal to second, third and fourth antennal segments combined (longer in *cyanella*, shorter in *simillima*); flagellar segments 2 to 11 each less than twice as long as wide (moniliform in *simillima*); hypostomal carina usually low and uniform. Middle leg with tarsal segments not swollen; hind basitarsus three to four times as long as wide, narrow at base, gradually widened toward apex, which is often considerably wider than base, not toothed; hind tibial spurs distinctly curved at tips (straight in *cyanella*); strigilis with inner apical angle of velum rounded; apex of velum usually truncate; concavity of inner margin of velum shallow to moderately deep; apex of malus produced into a short spine. Forewing cells usually with dense and short hair (longer in *albolateralis*), distal portion finely papillate, often with hairs similar to those of cells, vein A equal to or less than twice as long as vein B. Metasomal terga 2 to 5 with apical impunctate bands wide (narrow to moderately wide *cyanella*, and *rostrata*); apical margin of tergum 6 with shallow to deep median emargination usually clearly defined; tergum 7 with apex produced, midapex with emargination, forming two teeth (two lobes in *juxta*). Metasomal sternum 1 with apical margin broadly rounded, midapex not emarginate (except in *rostrata*); sternum 2 with apex usually strongly convex, often with midapical third or fourth subtruncate; sternum 2 large, largely covering third; median third of sternum 3 with an emargination which is fringed with long hairs; sternum 4 with midapical third produced, subtruncate or rounded, posterior median portion with long hairs which are usually bent mesad, apical margin uniformly convex or with middle third subtruncate; sternum 6 broadly sub-

triangular; sternum 8 with apical half more broadly subtriangular than basal half, tip may be acuminate. Gonocoxite never greatly widened (except at angle in *atrocyanea*), without subapical process.

Female.—Length of body 10 to 13 mm. Color of body dark blue with purplish or greenish tinge. Pubescence short, not loosely branched, mixed black and white or entirely black; metasomal terga without subapical or apical fasciae (except in *seclusa*); scopa black (fuscous in *rostrata*). Mandible broad, weakly or strongly constricted distad of base, gradually widened to apex which is slightly wider than constriction (in *cyaneonitens* and *rawlinsi* apex nearly twice as wide as width of constriction), lacking protuberance or transverse ridge near base (except in *atrocyanea, rostrata, sculleni,* and *seclusa,* which have a low transverse ridge like that of some species of *Centrosmia*), apex with four teeth, tooth 2 often considerably smaller than others; distance between teeth 1 and 3 greater than distance between 3 and 4; eye usually considerably narrower than genal area; inner margins of eyes slightly to moderately converging; clypeus with punctures confluent, truncation not thickened (with small median angle in *sculleni,* large median projection in *rostrata),* usually longer than margin from end of truncation to lateral angle of clypeus; malar space absent; hypostomal carina strongly elevated, abruptly reduced just behind or well behind angle forming a distinct tooth. Hind basitarsus three to four times as long as wide, usually wider in the middle than at the base or apex, apex subtruncate to truncate; hind tibial spurs strongly curved at tips. Forewing cells usually with short, dense hairs, in some species longer hairs scattered in different areas. Metasomal terga 2 to 5 with apical impunctate bands wide (narrower in *cyanella*); tergum 6 with apical margin forming a flange.

Species included: *Osmia (Monilosmia) albolateralis* Cockerell, *atrocyanea* Cockerell, *brevis* Cresson, *bridwelli* Sandhouse, *cara* Cockerell, *cyanella* Cockerell, *cyaneonitens* Cockerell, *densa* Cresson, *gabrielis* Cockerell, *hendersoni* Cockerell, *juxta* Cresson, *rawlinsi* Sandhouse, *rostrata* Sandhouse, *sculleni* Sandhouse, *seclusa* Sandhouse, *simillima* Smith.

The subgenus *Monilosmia* is largely restricted to the western half of North America, but *O. simillima* ranges eastward to the Atlantic in Canada and the northern part of the United States. Unfortunately the type species of the subgenus is quite aberrant, particularly in the male, and is typical of the group only in a nomenclatorial sense.

Subgenus *Centrosmia* Robertson

Centrosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 165, 166, 170. *Type species: Osmia bucephala* Cresson, 1864, original designation and monobasic.

Robertson proposed this name in his key to the genera of the subfamily Osmiinae (Family: Megachilidae) for the single species, *Osmia bucephala* Cresson. Sandhouse grouped *bucephala, nigriventris*, and *O. (Chenosmia) inermis* in the subgenus *Melanosmia*, with the remark "Although this subgenus is based chiefly on differences of color, both of integument and pubescence, and no single structural character is common to all of the included species, it is retained as a convenient group for three species of this fauna, two of which are holarctic." *O. bucephala* and *nigriventris* are here removed from *Melanosmia* because of the pattern of the seventh and eighth metasomal sterna, and genitalia of the male, and because of the swollen apical margin of clypeus, and the presence of a ridge across the base of each mandible in the female. In the above mentioned characters, *bucephala* and *nigriventris* agree with a group of species placed in the subgenus *Nothosmia* by Sandhouse, and here united under the name *Centrosmia.*

Male.—Length of body 7 to 17 mm. Pubescence white, usually with black intermixed; metasomal terga without apical or subapical fasciae. Mandible widest at base, narrowest at region of constriction which is more than half as wide as apex, with V-shaped notch separating long, lower tooth from truncate or oblique, acute, upper tooth; width of genal area equal to or wider than eye; inner margins of eyes slightly to distinctly converging anteriorly; clypeus thickly covered with white hairs arising from confluent punctures, margin weakly wavy with one or two weak median anterior projections, apical margin narrowly impunctate; scape equal to antennal segments 2 to 4 combined (except in *bucephala* and *pikei* where scape shorter); flagellar segments 2 to 11 each less than twice as long as wide (more than twice as long as wide in *bucephala*); hypostomal carina not greatly produced, usually low and slightly raised behind angle. Middle leg with second and third (also fourth in *bucephala*) tarsal segments greatly swollen (except in *bakeri* and *nigriventris*); basitarsus of hind leg three to four or more times as long as wide, parallel sided, broadest medially, or gradually narrowed towards apex (in *bucephala* and *nigriventris* widest near apex, narrowed towards base); strigilis with inner apical angle of velum rounded, apex truncate to slightly oblique; apex of malus

produced to a sharply pointed spine; concavity on inner margin of velum shallow or absent. Forewing with pubescence of cells usually sparse and short (longer in *austromaritima*), apex papillate, vein A longer than vein B (except in *pikei* where A may be nearly subequal to B). Metasomal terga 2 to 5 with broad apical impunctate bands; apical margin of 6 with or without shallow undefined emargination or truncation; apex of 7 produced, midapex of projection emarginate, forming two blunt, wide lobes (except *austromaritima* which has two sharp teeth). Metasomal sterna 1 and 2 with posterior margins arcuate (first with midapical emargination in *vandykei* and *austromaritima*); sternum 2 large, largely covering sternum 3; median apical third of sternum 3 with an emargination which is fringed with long hairs; midapical half or third of sternum 4 produced and truncate or rounded, usually with a median apical patch of bristle-like hairs bent mesad at tips; sternum 6 with a midapical projection with or without a patch of bristles on projection; sternum 8 subtriangular with apical process usually long and slender of varying length. Gonocoxite without a process arising before apex (*bucephala* with subapical ventral angle produced); distal portion of gonocoxite abruptly narrowed, slender, hairless; apex of volsella subtriangular (rounded in *bakeri*).

Female.—Length of body 9 to 16 mm. Metasomal terga without apical or subapical fasciae. Scopa black. Mandible gradually widened to apex which is much less than twice as wide as width of constriction; mandible with transverse ridge or protuberance near base; apex with second tooth rudimentary (large in *nigriventris*); distance between teeth 1 and 3 greater than distance between 3 and 4, eye narrower than genal area, inner margins of eyes slightly converging to diverging; clypeus with punctures confluent, truncation thickened, longer than distance from end of truncation to lateral angle of clypeus; malar space absent (present in *bucephala*); hypostomal carina greatly to moderately elevated, highest just behind to well behind angle, lower at angle so that tooth (sometimes low and rounded) is formed behind angle. Hind basitarsus between three and four times as long as wide, almost uniformly wide throughout, apex truncate; hind tibial spurs curved at tips. Forewing cells with hairs fine, sparse, dense in certain areas, papillae on distal part fine, dense. Metasomal terga 2 to 5 with apical impunctate bands, finely lined; tergum 6 with apical margin forming a flange.

Species included: *Osmia (Centrosmia) austromaritima* Michener,

bakeri Sandhouse, *bucephala* Cresson, *nigriventris* (Zetterstedt), *pikei* Cockerell, *raritatis* Michener, *tanneri* Sandhouse, *thysanisca* Michener, *vandykei* Sandhouse.

This subgenus is known only from North America, except for *nigriventris* which occurs also in northern and alpine Europe. The species have recently been revised by Sinha and Michener (1958).

Trichinosmia, new subgenus

Type species: *Osmia latisulcata* Michener, 1936.

Sandhouse (1939) included *Osmia latisulcata* in the subgenus *Nothosmia*. This species differs, however, from all other subgenera, including *Nothosmia*, in having the following combination of characters: head and thorax with unusually long, branched hair; terga without impunctate bands; forewings with long, sparse hair; in the male, flagellar segments 2 to 11 each twice as long as wide, scape shorter than antennal segments 2 to 4 combined, gonocoxite and penis valve of uniform width, the former with scanty, sparse hairs; in the female, clypeal margin tridentate (much as in *sculleni*), head as long as broad, terga 2 to 6 with apical bands of simple hair, and strigilis with an unusually long apical malar spine (one-third of entire malus).

Male.—Length of body 10 mm. Pubescence white, with black intermixed in a few areas, hairs with long branches on head and thorax; metasomal terga with apical fasciae of simple hair. Mandible moderately wide, widest at base, narrower and uniformly wide at region of constriction and apex, with V-shaped notch separating long lower tooth from acute upper tooth; width of genal area subequal to that of eye; inner margins of eyes slightly converging anteriorly; clypeus with margin truncate, weakly wavy, with apical margin moderately broadly impunctate; scape shorter than antennal segments 2 to 4 combined; flagellar segments 2 to 11 each at least twice as long as wide; hypostomal carina low, slightly higher well behind angle. Middle leg with mediotarsal segments not swollen; hind basitarsus about three times as long as wide, not toothed, parallel sided; strigilis with inner apical angle of velum rounded, apex of malus produced into a long, moderately sharp spine, inner margin of velum deeply emarginate. Forewing cells with sparse and long hair, distal portion with hairs longer than in any other subgenus, vein A much less than twice as long as vein B. Metasomal terga 2 to 5 without impunctate bands; apical margin of tergum 6 with a moderately deep well defined emargination; apex of tergum 7

produced, midapical production weakly emarginate forming two short teeth. Metasomal sterna 1 and 2 with apical margins broadly rounded, median third of each subtruncate; sternum 3 with median emargination, fimbria extending beyond apex; sternum 4 with apical margin slightly convex, with a short, stout, median projection; sternum 8 with basal half triangular, apical half broadly rounded. Gonocoxite of nearly uniform width throughout length, slightly curved, without subapical swelling, similar to that of subgenus *Cephalosmia,* apex of volsella subtriangular.

Female.—Length of body 12 to 13 mm. Pubescence on head and thorax with long branches, simple hair on metasomal terga, color mixed black and white; scopa black. Mandible moderately broad, weakly constricted distal to base, gradually widened to apex which is strongly oblique and less than twice as wide as width of constriction, base of mandible lacking transverse ridge or protuberance, apex with four teeth, teeth 1 and 2 almost confluent, 3 and 4 narrowly triangular, distance between 1 and 3 slightly greater than distance between 3 and 4; eye subequal to width of genal area; inner margins of eyes subparallel or weakly converging anteriorly; clypeus with punctures confluent, truncation not thickened, with one median and two lateral teeth, much longer than margin from end of truncation to lateral angle of clypeus; malar space absent; scape shorter than antennal segments 2 to 4 combined; hypostomal carina moderately high, abruptly reduced behind angle forming weak tooth as in some *Monilosmia.* Hind basitarsus nearly four times as long as wide, subparallel sided; hind tibial spurs almost straight, forewing with hairs on distal part and cells sparse and longer than those of any other subgenus. Metasomal terga 2 to 5 without apical impunctate bands, *with simple erect hairs;* tergum 6 with apical margin forming a flange.

Osmia (Trichinosmia) latisulcata Michener is the only species included in this subgenus. It is restricted to Western North America.

Subgenus *Cephalosmia* Sladen

Cephalosmia Sladen, 1916, Canad. Ent., vol. 48, p. 270; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 21. *Type species: Osmia armaticeps* Cresson, 1878 = *Osmia montana* Cresson, 1864, monobasic.

This subgenus is recognized by the following combination of characters: The head is long and the genal area very wide; the hypostomal carina is high, in the female not abruptly reduced behind the angle; the superior mesal portion of the carina border-

ing the antennal socket is more strongly developed than the rest of the carina; the female has a carina on the inner surface of the mandible which arises near the superior basal angle and extends obliquely to the inferior margin, where it ends abruptly about halfway between the base and the apex; the metasomal terga of the female are weakly convex and densely punctured, the apical margin of the sixth being strongly curved and without a wide apical flange. In the male sterna 2 and 3 have the apical margins truncate or subtruncate, sternum 2 only slightly overlapping the base of sternum 3; the base of sternum 6 has a deep triangular emargination, the apical margin bears a strong triangular or rounded median projection.

Male.—Length of body, 8 to 13 mm. Pubescence black or black and white intermixed. Mandible widest at base, narrower at region of constriction which is slightly wider than apex, with V-shaped notch separating long (short in some species) lower tooth from triangular, acute, upper tooth; eye slightly narrower than genal area; inner margins of eyes slightly to distinctly converging anteriorly; clypeus covered with white hairs arising from confluent punctures, margin produced, often convex, median portion weakly wavy or dentate, with apical impunctate band narrow to moderately wide; scape subequal to or slightly shorter than antennal segments 2 to 4; segments 2 to 11 unmodified, each less than twice as long as wide (in *montana* nearly twice as long as wide); *superior mesal portion of carina bordering antennal foramen more strongly developed than rest of carina;* hypostomal carina never high, moderately raised a little behind angle. Middle leg with tarsal segments 2 and 3 not swollen; hind basitarsus four times as long as wide or slightly less, uniformly wide or wider in distal portion, not toothed; strigilis with apical margin of velum truncate or rounded, apex of malus produced into a short to moderately long, narrow spine, concavity on inner margin of velum moderately deep. Forewing cells with long or short, sparse hairs, distal portion of wing finely papillate, vein A usually less than twice as long as vein B. Metasomal terga 2 to 5 with apical impunctate bands wide; tergum 6 with shallow to deep clearly defined emargination; tergum 7 with apex produced, midapex of projection emarginate, forming two triangular teeth. Metasomal sternum 1 with apical margin weakly convex, median portion with a wide, shallow emargination; sterna 2 and 3 with apical margins truncate or subtruncate; sternum 2 not covering sternum 3; sternum 4 with median third of apical margin usually

produced, apex of projection rounded or truncate, fringed with dense, short, black hairs; base of sternum 6 with a deep triangular emargination, apical margin with a strong triangular or rounded median projection, basal half of eighth sternum broadly triangular, distal half with sides subparallel basally, then strongly converging, apex subtriangular and fringed with bristles. Gonocoxite thick, tapering slightly from base to apex, lateral surface of apical third beset with hairs, some hairs on mesal surface near apex; free portion of volsella rather narrow, subtriangular.

Female.—Length of body 10 to 17 mm. Pubescence black or mixed black and white; scopa black. Mandible broad, constricted distal to base, gradually widened to apex which is one and one half to two times as wide as width at constriction, base without transverse ridge or protuberance (except in *quadriceps*), with four distinct teeth, teeth 3 and 4 triangular, 1 and 2 subtriangular to broadly rounded, distance between 1 and 3 much longer than distance between 3 and 4; *inner surface of mandible with a carina which arises near upper basal angle and extends obliquely to lower margin, where it ends abruptly about half way between base and apex;* genal area much wider than eye which is more than twice as long as wide; inner margins of eyes slightly converging to slightly diverging; clypeus (shortened and modified in *montana* and *quadriceps*) with punctures separated or nearly absent, with truncation shorter than margin from end of truncation to lateral clypeal angle, apical margin simple or modified; *mesosuperior portion of carina bordering antennal socket more strongly developed than rest of carina;* hypostomal carina low to moderately high, highest immediately or well behind angle where it forms a rounded tooth; hind basitarsus four to five times as long as wide, of uniform width throughout or tapering slightly, apex truncate to broadly rounded; hind tibial spurs straight to weakly curved distally. Forewing with hairs on cells scanty, usually short and sparse, distal part with fine, dense or sparse papillae. Metasomal terga 1 to 5 with apical impunctate bands moderately wide; tergum 6 not flanged or rarely with a weak flange.

Species included: *Osmia (Cephalosmia) californica* Cresson, *grinnelli* Cockerell, *marginipennis* Cresson, *mendocinensis* Sandhouse, *montana* Cresson, *pascoensis* Cockerell, *quadriceps* Cresson, *subaustralis* Cockerell.

This subgenus is restricted to western North America.

Subgenus *Chalcosmia* Schmiedeknecht

Osmia (Chalcosmia) Schmiedeknecht, 1886, Apidae Europaeae, vol. 2, p. 886; Ducke, 1900, Berichte des naturwissenschaftlich-medizinischen Vereines in Innsbruck, vol. 25, p. 16; Friese, 1911, Das Tierreich, vol. 28, p. 108; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 13. *Type species: Apis fulviventris* Panzer, 1798, designation of Sandhouse, 1939.

Gnathosmia Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 165, 171; Cockerell, 1912, Proc. U. S. Nat. Mus., vol. 42, p. 216. *Type species: Osmia georgica* Cresson, 1878, original designation and monobasic.

This subgenus can be recognized by the following characters: In the male the fourth metasomal sternum is thickened at the apical margin, the lateral portions have narrow transverse sulci (visible in posterior view), and each hind basitarsus bears a tooth. In the female the clypeal margin is thickened or otherwise modified and provided with two small sockets, each giving rise to a tuft of hair, mesal to the two large lateral tufts. There is a transverse ridge or a protuberance near the base of the mandible in the female.

Male.—Length of body 8 to 13 mm. Pubescence white or slightly yellowish. Mandible moderately wide, widest at base, narrower at region of constriction which is almost as wide as apex, with V-shaped notch separating lower tooth from truncate or oblique, right angular or acute upper tooth; eye equal to or slightly wider than genal area; inner margins of eyes slightly to distinctly converging anteriorly; clypeus covered with white hairs arising from confluent punctures; clypeal margin with median portion slightly produced, wavy or dentate; clypeus with apical impunctate band narrow to moderately wide; scape subequal to second, third, and fourth antennal segments combined; flagellar segments 2 to 11 unmodified, each less than twice as long as wide; hypostomal carina low and raised slightly or considerably behind angle; middle leg with tarsal segments not swollen; hind basitarsus of uniform width, usually strongly toothed (tooth smallest in *coerulescens*), parallel sided; strigilis with apical margin oblique; apex of malus produced into log spine which is widest at base and gradually narrowed toward apex; concavity on inner margin of velum shallow to moderately deep. Cells of forewing with sparse (dense in some areas) and short hairs, distal portion finely papillate, vein A usually less than twice as long as vein B (A is equal to B in *texana*). Metasomal terga 2 to 5 with apical impunctate bands narrow to moderately wide, with subapical fasciae; apical margin of tergum 6 usually with rather shallow but clearly defined emargination; apex of tergum 7 produced, apex of projection emarginate, forming two

blunt teeth. Metasomal sternum 1 with apex broadly rounded; sternum 2 large, greatly produced with apical margin convex, covering most of third, usually a shallow emargination at midapex of produced portion; median apical third of third sternum with an emargination which is fringed with long hairs; midapical half or third of sternum 4 produced and subtruncate or rounded, with a median apical patch of long hairs usually not surrounding an impunctate area; *sternum 4 with apical margin thickened, lateral portion of margin thickened with a narrow transverse sulcus visible from behind;* sternum 6 with apical margin strongly to weakly produced medially; sternum 8 with base subtriangular, apical portion broadly convex. Gonocoxite wide, gradually narrowed toward the tip, bent mesally toward apex but not angulate, with neither swelling before distal portion nor subapical process; penis valve broad at base and gradually narrowed towards apex (in *coerulescens* gonocoxite uniformly slender throughout except at base, penis valve broad, of uniform width except at tip).

Female.—Length of body 10 to 16 mm. Scopa yellow or black; metasomal terga usually with subapical fasciae of plumose hair. Mandible broad, slightly constricted distal to base, gradually widened to apex, which is much less than twice as wide as width of constriction, with one or two protuberances or a transverse ridge near base of mandible, with four teeth; teeth 1, 3, and 4 triangular; tooth 2 obliquely truncate at apex (in *coerulescens* teeth one and two continuous); distance between teeth 1 and 3 subequal to or greater than distance between teeth 3 and 4; eye subequal to or much narrower than genal area; inner margins of eyes slightly converging to diverging; clypeus shortened and modified in native American species, punctures usually confluent, truncation longer than margin from end of truncation to lateral angle of clypeus, apical margin thickened or otherwise modified, *two small round tufts of bristles mesal to usual broad lateral tuft;* hypostomal carina high and abruptly reduced a short distance behind angle; hind basitarsus at least three times as long as wide, apex rounded (in *coerulescence* subtruncate); hind tibial spurs slightly curved distally. Forewing with hairs of cells short, fine, dense, sparse in some areas, papillae on distal part fine, dense; terga 1 to 5 without apical impunctate bands; tergum 6 with apical margin forming a broad flange.

North American species included: *Osmia (Chalcosmia) chalybea* Smith, *coerulescens* (Linnaeus), *coloradensis* Cresson, *georgica* Cresson, and *texana* Cresson.

Old World species examined and included in this subgenus: *Osmia (Chalcosmia) aurulenta* (Panzer), *coerulescens* (Linnaeus), *decemsignata* (Radoszkowski), *dimidiata* Morawitz, *latreillei* Spinola, *leucogastra* Morawitz, *leaiana* Kirby, *medanae* Magretti, *notata* (Fabricius), *rubicola* Friese, and *vidua* Gerstaecker.

The four native American species of *Chalcosmia* seem to be quite distinct from the fifth, *coerulescens,* which is probably introduced from Europe.

Group I (*chalybea, coloradensis, georgica* and *texana*) is characterized by the strongly developed upper margins of the two mesal sockets on the apical margin of the clypeus and the strongly developed protuberances near the base of the mandible in the female; and by the distinctly pointed tooth on each hind basitarsus, the thickened apical margin of the fourth metasomal sternum and the broad and apically tapering gonocoxite in the male.

Group II (*coerulescens*) is characterized by the unmodified margins of the two mesal sockets on the apical margin of the clypeus and the lack of or the extremely weak protuberance near the base of the mandible in the female; and by the extremely weak tooth on the hind basitarsus, the scarcely thickened apical margin of the fourth metasomal sternum and the uniformly slender gonocoxite in the male.

The Old World species can be placed in several groups. *O. aurulenta, decemsignata, medanae, notata* and *vidua* agree fairly well with *coerulescens* and may be placed in group II. The other species listed belong in two or three other groups.

Subgenus *Osmia* Panzer, s. str.

Osmia Panzer, 1806, Kritische Revision der Insekten-faune Deutschlands, vol. 2, p. 230; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 9; Michener, 1941, Amer. Midland Nat., 26: 163. *Type species: Anthophora bicornis* Linnaeus, 1758, = *Apis rufa* Linnaeus, 1758, designation of Latreille, 1810.

Amblys Klug, 1907, Illiger's Mag. f. Insektenkunde, vol. 6, pp. 198. *Type species: Apis bicornis* Linnaeus, 1758, = *Apis rufa* Linnaeus, 1758, by designation of Latreille, 1811.

Ceratosmia Thomson, 1872, Hymenoptera Scandinaviae, vol. 2, p. 232; Schmiedeknecht, 1884-86, Apidae Europaeae, vol. 2, p. 885; Ashmead, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 74; Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, pp. 165; Cockerell, 1912, Proc. U. S. Nat. Mus., vol. 42, p. 216; Sandhouse, 1939, Mem. Ent. Soc. Washington, vol. 1, p. 9. *Type species: Apis bicornis* Linnaeus, 1758, = *Apis rufa* Linnaeus, 1758, by designation of Sandhouse, 1939.

Aceratosmia Schmiedeknecht, 1884-86, Apidae Europaeae, vol. 2, p. 885. *Type species: Osmia emarginata* Lepeletier, 1841, by designation of Sandhouse, 1939.

Pachyosmia Ducke, 1900, Berichte des naturwissenschaftlich-medizinischen Vereines in Innsbruck, vol. 25, p. 18. *Type species: Apis rufa* Linnaeus, 1758, by designation of Sandhouse, 1939.

The subgenus *Osmia* can be easily distinguished from all other subgenera in having long and loosely branched pubescence; a distinct malar space, especially in the female; a round or elongate depression in the genal area of the female immediately below the eye; unmodified flagellar segments which, in the male, are twice as long as wide; a projection (weak in *ribifloris*) on the lower margin of the middle femur of the male; and male genitalia with elongate penis-valves provided with long ventral openings, and gonocoxites lacking hairs on the mesal surfaces.

Male.—Length of body 8 to 11 mm. Pubescence white with black intermixed, or largely black. Metasomal terga without apical or subapical fasciae. Mandible widest at base, narrowest at region of constriction which is almost as wide as apex, with V-shaped notch separating lower tooth from acute upper tooth; eye subequal to width of genal area; inner margins of eyes converging anteriorly; clypeus thickly covered with white hairs arising from fine, confluent punctures, margin weakly wavy or serrate in median third, with moderately broad apical impunctate band; scape shorter than antennal segments 2 to 4 combined; flagellar segments 2 to 11 unmodified, each over twice as long as wide; hypostomal carina not greatly elevated, uniform or often slightly raised behind angle; middle leg with tarsal segments not swollen, *femur with a projection on lower margin* (weak in *ribifloris*); basitarsus of hind leg four to five times as long as wide, not toothed, parallel sided; strigilis with apical margin of velum truncate, inner apical angle of velum rounded, concavity on inner margin of velum deep, apex of malus may be produced into a long, sharp pointed spine. Forewing cells with moderately short, sparse hair, apical portion papillate, vein A is two to three times as long as vein B. Metasomal terga 2 to 5 with impunctate bands, at least on posterior terga, tergum 6 with apical margin lacking emargination, turned up, forming a flange; tergum 7 with apex produced, midapex with shallow, wide emargination, forming two short lobes; metasomal sternum 1 broadly rounded without midapical emargination; sternum 2 with apical margin strongly convex and usually largely concealing sternum 3; sternum 3 with a wide and deep emargination; sternum 4 with apical margin broadly convex; apical margin of sternum 6 with a wide, median subtriangular production; sternum 8 with apical half narrowly triangular or broadly subtriangular. Gonocoxite long, slender, with no hairs on mesal surface; volsella broadly conical; penis valve long, tapering strongly apically, nearly reaching to exceeding apices

of gonocoxites (as in some *Chalcosmia*), *ventral opening extending nearly to apex.*

Female.—Length of body, 8 to 13 mm. Pubescence long, loosely branched, mixed black and white; metasomal terga without apical or subapical fimbriae; scopa black. Mandible broad, slightly constricted distad of base, gradually widened to apex, which is strongly oblique and twice as broad as constriction (in *lignaria*) or only slightly oblique and less than twice as wide as constriction (in *ribifloris*); eye much narrower than genal area; inner margins of eyes parallel to slightly diverging; clypeus (short and modified in *lignaria*) with punctures confluent, truncation simple or much modified, broader than margin from end of truncation to lateral angle of clypeus; *malar space distinct* (see also *bucephala*); *a round or elongate depression in genal area just below eye;* hypostomal carina not greatly elevated, highest well behind angle; basitarsus of hind leg three to four times as long as wide, of uniform breadth or a little widened in middle, apical margin truncate to slightly rounded; hind tibial spurs weakly curved. Forewing cells with long and short hairs intermixed, sparse, dense in some areas, distal part with papillae fine, dense. Terga 2 to 5 with apical impunctate bands narrow or absent; tergum 6 with apical margin forming a flange.

Species of *Osmia* proper are widespread in North America and Eurasia.

American species: *Osmia (Osmia) lignaria* Say, *ribifloris* Cockerell.

The Old World species examined and included in this subgenus: *Osmia (Osmia) cornuta* Latreille, *emarginata* Lepeletier, *kohlii* Ducke, *longicornis* Morawitz, *rufa* Linnaeus, *taurus* Smith, *tricornis* Latreille.

American Species of *Osmia* of Doubtful Position

In the course of examining species of the genus *Osmia* the author came across several which for some reason or other can not be definitely placed as to subgenus. An annotated list of these species is given below. Specimens of the species marked with asterisks were not seen by the author. Comments about these are based upon the published descriptions.

Osmia aglaia * Sandhouse, *Chenosmia* or *Monilosmia?*

Osmia angustipes * Cockerell, *Chenosmia?*

Osmia cockerelli Sandhouse, *Chenosmia?*

Osmia enixa * Sandhouse. White (1951) placed the female described as this species under *O. (Acanthosmioides) francisconis,* but

excluded the male from *Acanthosmioides*. The present author agrees with White in this decision. The species may be a *Chenosmia*.

Osmia felti Cockerell, *Monilosmia?*

Osmia foxi * Cameron. It is impossible to assign this species to subgenus from the description.

Osmia gaudiosa * Cockerell, *Chenosmia?*

Osmia grindeliae Cockerell. Only one specimen was examined by me. It is 10 mm. long and has a moderately sharp tooth on the hypostomal carina. The genal area is wider than the eye. But the clypeal truncation is equal to the lateral margin of the clypeus. Thus it can not be definitely placed under *Monilosmia* until more specimens are studied.

Osmia hemera Sandhouse, *Chenosmia?*

Osmia hesperos Sandhouse, *Monilosmia?*

Osmia inurbana Cresson, *Chenosmia?*

Osmia iridis Cockerell and Titus, *Monilosmia?*

Osmia lacus Sandhouse, *Chenosmia?*

Osmia melanopleura * Cockerell, *Chenosmia?*

Osmia mertensiae Cockerell, *Chenosmia?*

Osmia mixta * Michener, *Monilosmia* or *Chenosmia?*

Osmia nelsoni * Cockerell, *Monilosmia?*

Osmia nigritula * Friese. It is impossible to assign this species to any subgenus from the description.

Osmia novaescotiae * Cockerell, *Monilosmia?*

Osmia pacifica * "Say," Packard, cannot be assigned to any subgenus.

Osmia paradisica Sandhouse, *Monilosmia?*

Osmia phenax * Cockerell, *Nothosmia?*

Osmia pulsatillae Cockerell, *Chenosmia?*

Osmia pusilla Cresson, *Chenosmia?*

Osmia solitaria * Sandhouse, *Monilosmia?*

Osmia stasima * Lovell, *Nothosmia?*

Osmia virga Sandhouse, *Chenosmia?*

Osmia vallicola Cockerell, *Chenosmia?*

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It should be mentioned that while the classification here proposed does not agree with that of Sandhouse (1939), her work was most useful and was an essential basis for completion of the present study. In many cases characters which she used, and her expressions for their description, have been used with little change.

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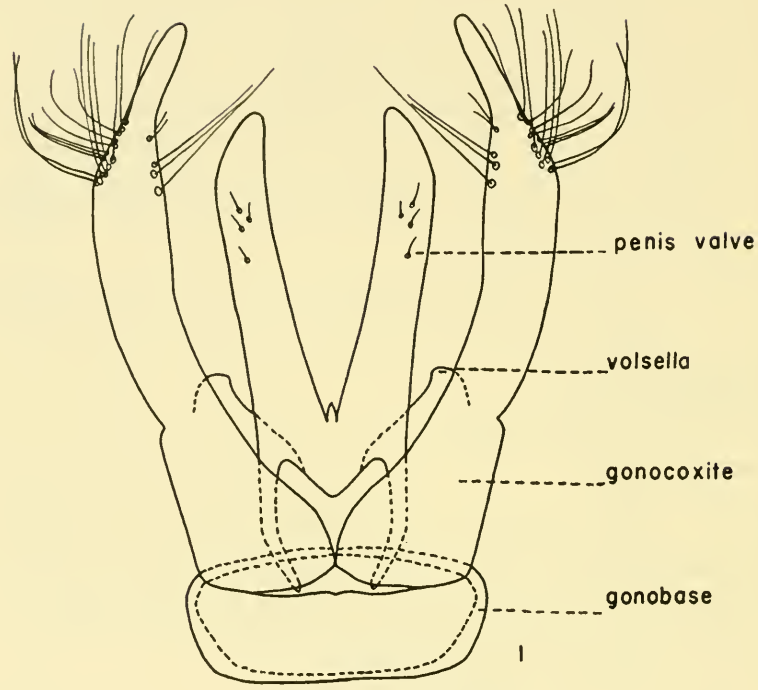


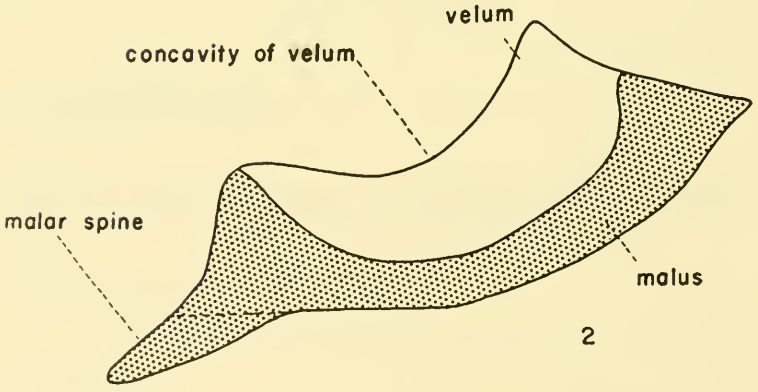
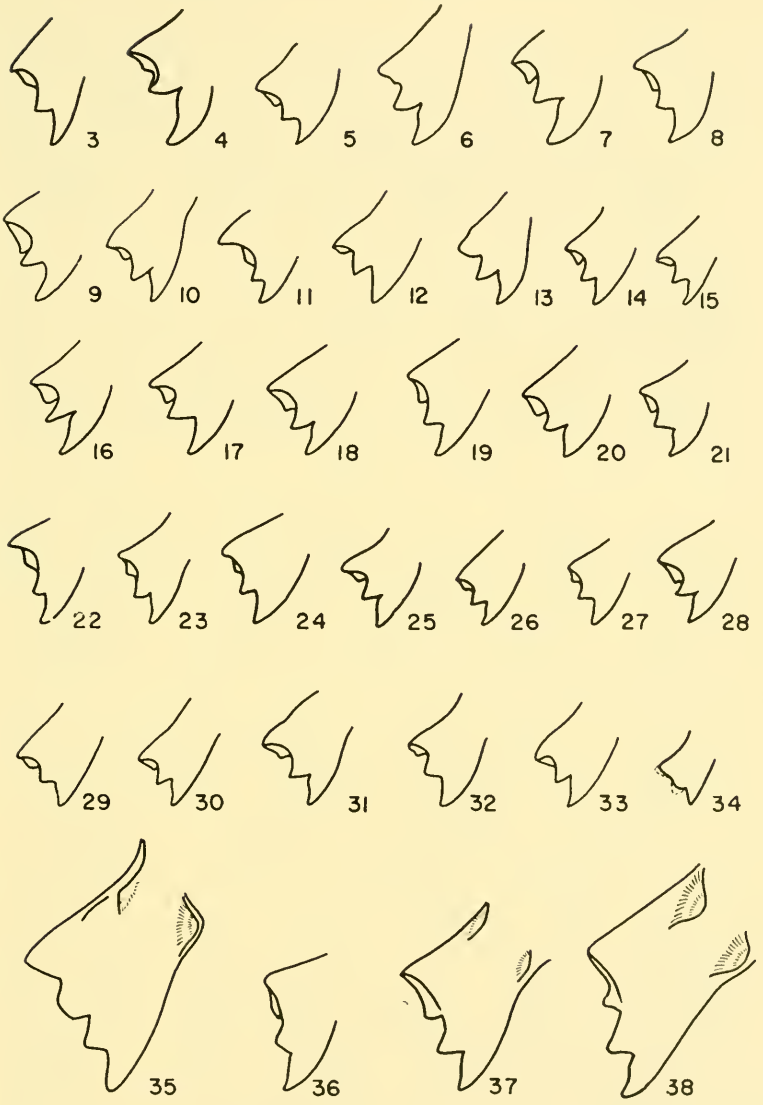
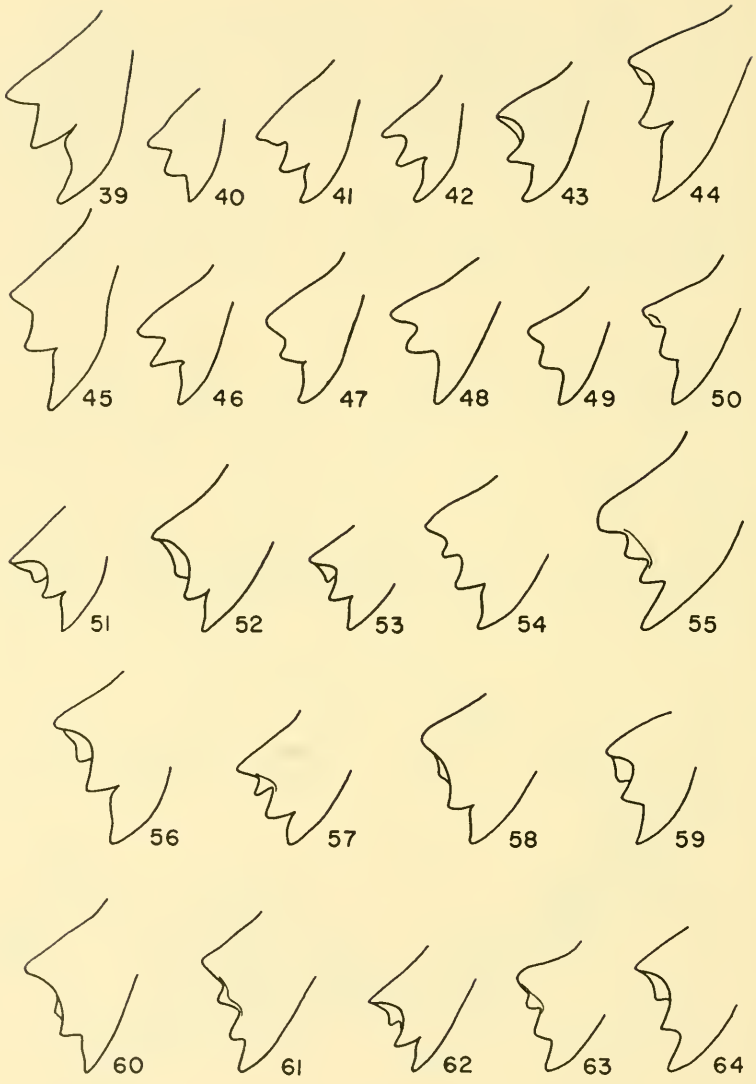


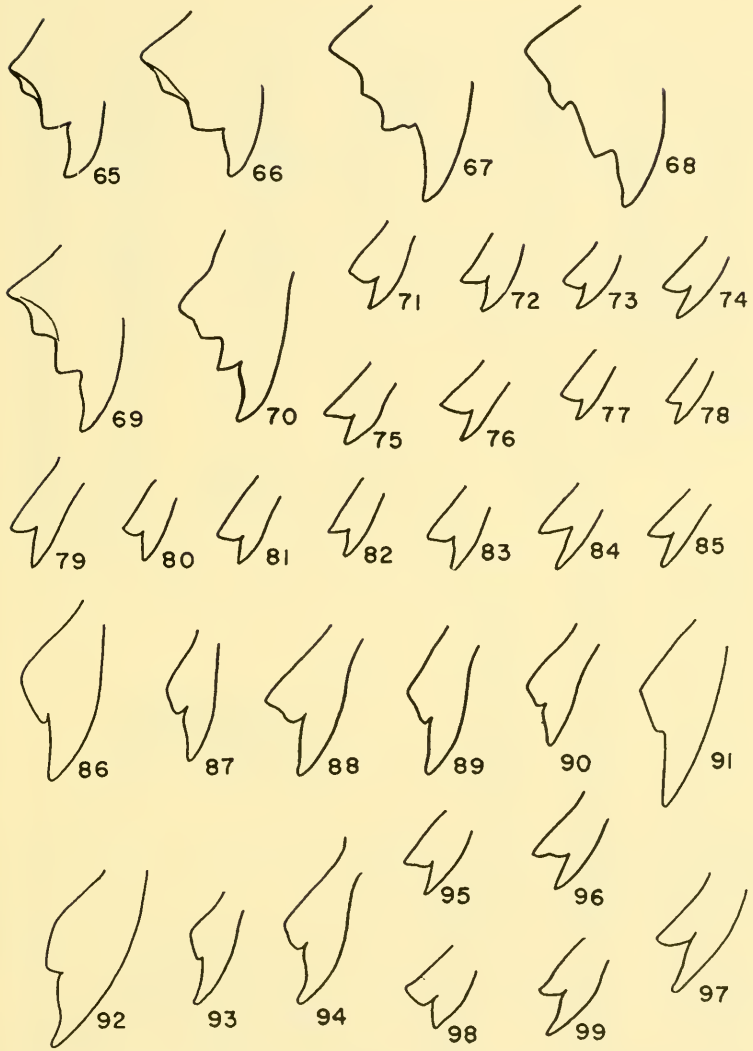
FIG. 1. Dorsal view of male genitalia, *O.* (*Nothosmia*) *albiventris.*
FIG. 2. Strigilis of female, *O.* (*Euthosmia*) *glauca.*



FIGS. 3-38. Apex of left mandible, female: 3, *O.* (*Diceratosmia*) *conjuncta*; 4, *subfasciata*; 5, O. (*Nothosmia*) *albiventris*; 6, *cerasi*; 7, *cordata*; 8, *distincta*; 9, *inspergens*; 10, *marginata*; 11, *pumila*; 12, *sandhouseae*; 13, *titusi*; 14, *O.* (*Chenosmia*) *calla*; 15, *caulicola*; 16, *clarescens*; 17, *cobaltina*; 18, *collinsiae*; 19, *cyanopoda*; 20, *dolerosa*; 21, *exigua*; 22, *illinoensis*; 23, *indeprensa*; 24, *laeta*; 25, *malina*; 26, *nanula*; 27, *pentstemonis*; 28, *proxima*; 29, *regulina*; 30, *sanctae-rosae*; 31, *tersula*; 32, *trevoris*; 33, *zephyros*; 34, *O.* (*Euthosmia*) *glauca*; 35, *O.* (*Chalcosmia*) *chalybea*; 36, *coerulescens*; 37, *coloradensis*; 38, *texana*.

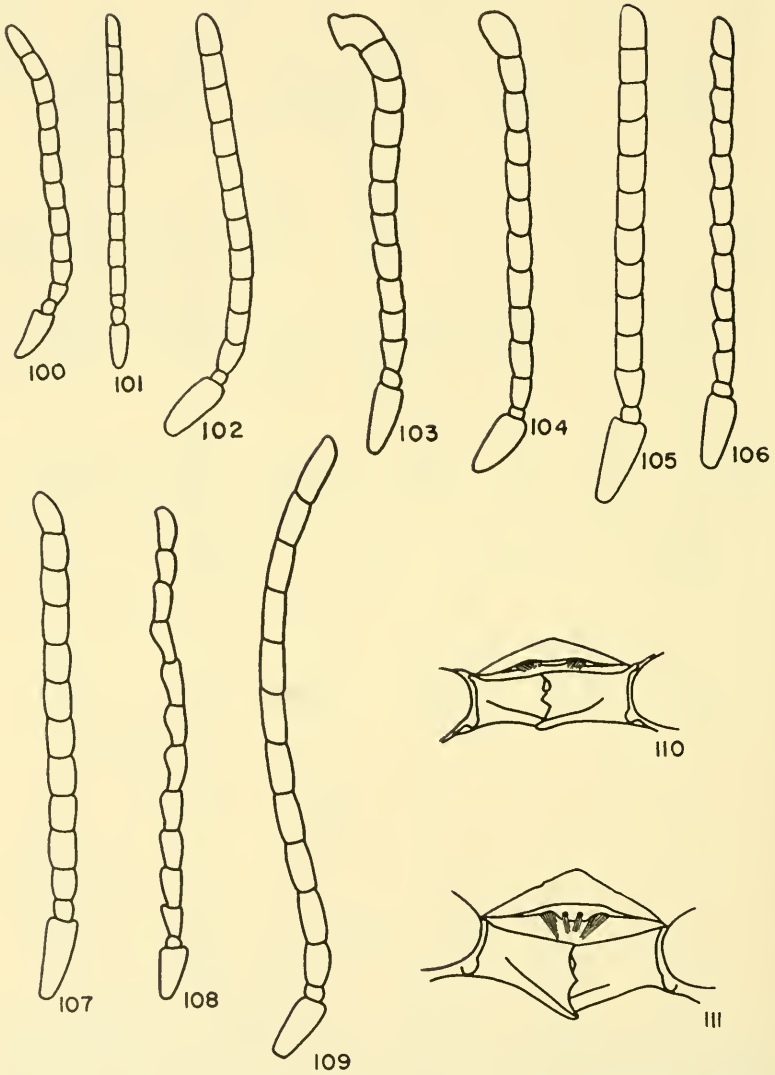


FIGS. 39-64. Apex of left mandible, female: 39, *O.* (*Acanthosmioides*) *calcarata*; 40, *dakotensis*; 41, *francisconis*; 42, *giliarum*; 43, *hurdi*; 44, *integra*; 45, *longula*; 46, *nifoata*; 47, *nigrifrons*; 48, *nigrobarbata*; 49, *physariae*; 50, *sedula*; 51, *O.* (*Monilosmia*) *albolateralis*; 52, *atrocyanea*; 53, *brevis*; 54, *bridwelli*; 55, *cara*; 56, *cyaneonitens*; 57, *densa*; 58, *gabrielis*; 59, *hendersoni*; 60, *rawlinsi*; 61, *rostrata*; 62, *sculleni*; 63, *seclusa*; 64, *simillima*.



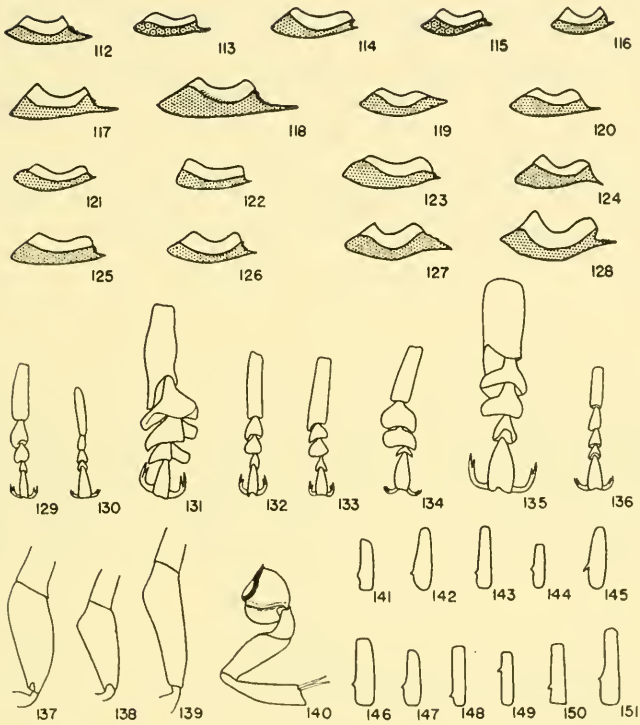
FIGS. 65-70. Apex of left mandible, female: 65, O. (*Cephalosmia*) *californica*; 66, *grinnelli*; 67, *pascoensis*; 68, *quadriceps*; 69, *subaustralis*; 70, *O.* (*Trichinosmia*) *latisulcata.*

FIGS. 71-99. Apex of mandible, male: 71, *O.* (*Diceratosmia*) *conjuncta*; 72, *subfasciata*; 73, *O.* (*Nothosmia*) *albiventris*; 74, *marginata*; 75, *titusi*; 76, *O.* (*Chenosmia*) *inermis*; 77, *pentstemonis*; 78, *O.* (*Euthosmia*) *glauca*; 79, *nemoris*; 80, *O.* (*Chalcosmia*) *coerulescens*; 81, *coloradensis*; 82, *O.* (*Centrosmia*) *bakeri*; 83, *pikei*; 84, *vandykei*; 85, *thysanisca*; 86, *O.* (*Acanthosmioides*) *calcarata*; 87, *griffardi*; 88, *integra*; 89, *kenoyeri*; 90, *lanei*; 91, *longula*; 92, *nigrobarbata*; 93, *obliqua*; 94, *sladeni*; 95, *O.* (*Monilosmia*) *brevis*; 96, *simillima*; 97, *O.* (*Cephalosmia*) *marginipennis*; 98, *montana*; 99, *O.* (*Trichinosmia*) *latisulcata.*



FIGS. 100-109. Antenna of male: 100, *O.* (*Chenosmia*) *pentstemonis*; 101, *O.* (*Euthosmia*) *glauca*; 102, *nemoris*; 103, *O.* (*Centrosmia*) *vandykei*; 104, *O.* (*Acanthosmioides*) *giffardi*; 105, *integra*; 106, *odontogaster*; 107, *O.* (*Monilosmia*) *juxta;* 108, *simillima;* 109, *O.* (*Osmia*) *lignaria.*

FIGS. 110-111. Anteroventral view of head, female: 110, *O.* (*Chenosmia*) *pentstemonis*; 111, *O.* (*Chalcosmia*) *coerulescens.*



FIGS. 112-128. Strigilis of male: 112, *O.* (*Diceratosmia*) *conjuncta*; 113, *O.* (*Nothosmia*) *pumila*; 114, *sandhouseae*; 115, *O.* (*Chenosmia*) *regulina*; 116, *O.* (*Euthosmia*) *glauca*; 117, *nemoris*; 118, *O.* (*Chalcosmia*) *chalybea*; 119, *coerulescens*; 120, *O.* (*Centrosmia*) *austromaritima*; 121, *bakeri*; 122, *thysanisca*; 123, *vandykei*; 124, *O.* (*Acanthosmioides*) *odontogaster*; 125, *O.* (*Monilosmia*) *brevis*; 126, *O.* (*Cephalosmia*) *montana*; 127, *O.* (*Trichinosmia*) *latisulcata*; 128, *O.* (*Osmia*) *lignaria*.

FIGS. 129-136. Tarsus of left middle leg, male: 129, O. (*Centrosmia*) *austromaritima*; 130, *bakeri*; 131, *bucephala*; 132, *thysanisca*; 133, *pikei*; 134, *vandykei*; 135, *O. longula*; 136, *odontogaster*.

FIGS. 137-139. Middle femur of male: 137, *O.* (*Monilosmia*) *atrocyanea*; 138, *O.* (*Osmia*) *lignaria*; 139, *ribifloris*.

FIG. 140. Ventral view of posterior leg showing the carina on coxa, *O.* (*Diceratosmia*) *subfasciata*.

FIGS. 141-151. Posterior basitarsus of male: 141, *O.* (*Nothosmia*) *albiventris*; 142, *distincta*; 143, *marginata*; 144, *pumila*; 145, *sandhouseae*; 146, *titusi*; 147, *O.* (*Chenosmia*) *kincaidii*; 148, *O.* (*Chalcosmia*) *coerulescens*; 149, *coloradensis*; 150, *georgica*; 151, *O.* (*Monilosmia*) *densa*.

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Notes on Oviposition and the Hatching of Eggs of *Aedes* and *Psorophora Mosquitoes* (Diptera: Culicidae)[1]

BY

A. RALPH BARR and ABDULLA AL-AZAWI

ABSTRACT: This paper describes a technique for inducing oviposition of aedine mosquitoes. A theory concerning oviposition behavior of these mosquitoes is also presented. Finally, evidence is given to support the belief that "conditioning" and the presence of an adequate stimulus are necessary to promote hatching of the eggs of *Aedes* and *Psorophora* mosquitoes. Eggs of *Aedes canadensis* react differently than do those of the other species tested; they must be subjected to influences which are still unknown before hatching will take place.

INTRODUCTION

Information concerning the laying and hatching of aedine eggs is meager and conflicting. For this reason the senior author has been carrying out incidental studies on the hatching of *Aedes* eggs for several years. The results presented in this paper are strictly preliminary but give some interesting leads for future work and confirm some of the results of Horsfall (1956). In addition it is hoped that the present work will stimulate others to investigate this phase of mosquito biology.

MATERIALS AND METHODS

The mosquitoes used in this work were *Aedes vexans* (Meigen), *A. aegypti* (Linnaeus), *A. canadensis* (Theobald), *A. trivittatus* (Coquillett), *A. nigromaculis* (Ludlow), *A. cinereus* Meigen, *A. triseriatus* (Say), and *Psorophora longipalpis* Roth. Field-collected females of all species (except *A. aegypti*) were used. All mosquitoes were from Douglas Co., Kansas unless otherwise stated.

1. Contribution number 971 from the Department of Entomology, University of Kansas, Lawrence, Kansas.

Female mosquitoes were captured in test tubes (16 mm. diameter x 15 cm. length) while feeding in the field. They were demonstrated to have been inseminated either by examination of the spermathecae or by hatching some of their eggs (parthenogenesis does not normally occur in mosquitoes although it may be induced [Laven, 1956]).

The bottom of the test tube used for catching the mosquito was filled with moist cotton and was placed over the female while she was feeding. When she had finished feeding and had flown up into the tube, cheesecloth was used to close the mouth of the tube; it was secured with a rubber band. When a less porous material was used to close the tube moisture condensed in the tube which proved detrimental to the mosquito.

The test tubes with their occupants were stored on their sides in the laboratory at room temperature (24 to 26° C.); all experiments were carried out at this temperature. Females usually oviposited well after a single feeding; many refed readily through the cheesecloth and laid additional clutches of eggs. Females have also been kept in lamp-chimneys at times but were usually more reluctant to oviposit in such a container. The smaller size of the test tube probably "forces" oviposition to a certain extent.

All eggs laid were kept in contact with water for at least several days to prevent desiccation. They were then stored in an insectary at a relative humidity of about 70-90%. The eggs used in this study varied in age from about a week to two months; most were 2 to 4 weeks old. It would appear that the eggs do not become less viable in this length of time. All eggs were "conditioned" (*vide infra*) for at least four days unless otherwise stated.

INSEMINATION

In collecting eggs from mosquitoes one should first make certain that the mosquitoes have been inseminated. This can be quickly done by examining the spermathecae for the presence of spermatozoa. Throughout this work females have been checked from time to time and it has been found that the *Aedes* and *Psorophora* females taken attacking man in the field almost invariably have been inseminated. An example is given from data collected in Minnesota in June and July of 1952. Dissections were made of 24 females of *Aedes vexans* and 4 *A. cinereus*. All 28 females had been inseminated; in most cases the large and one of the small spermathecae contained spermatozoa. The second small spermatheca was usually

either empty or contained only a few spermatozoa. (Occasionally a female had spermatozoa only in the large spermatheca or in all three spermathecae.) All of these females were in practically perfect condition (*i. e.,* were almost entirely unrubbed) indicating that they had emerged recently. In the species the authors have studied it appears that females usually mate within a short period after emergence, and usually before they seek a host.

RESULTS

OVIPOSITION

In early experiments the senior author encountered difficulty in inducing females to oviposit in the laboratory. With *Aedes aegypti* the substrate usually provided for oviposition is damp filter paper but most species of *Aedes* and *Psorophora* appear reluctant to oviposit on such a medium. This difficulty was inadvertently overcome when moist cotton was provided to humidify a cage; it was found that females oviposited readily on this medium. It seems likely that females which lay dormant eggs around the edges of ground pools actually insert their eggs into crevices in the ground; this process has been described for *Aedes nigromaculis* by Husbands and Rosay (1952). This would explain why such mosquitoes will oviposit readily on rough surfaces but not on smooth ones (Beckel, 1955); it would also explain why *Aedes polynesiensis* prefers to lay its eggs in creases in filter paper (Wallis, 1954). *Aedes aegypti* females, which frequently oviposit on smooth containers, probably are less fastidious in this respect. The authors have observed that *A. triseriatus,* a treehole mosquito, also prefers to lay its eggs in cracks in wood. If the above theory is correct, it might be predicted that the eggs of ground pool mosquitoes are more susceptible to the effects of drying than is true of *A. aegypti.* This point is being investigated further in this laboratory at the present time.

Most of the mosquitoes utilized fed once before depositing a clutch of eggs and laid about a hundred eggs after a period of about 6 days. A good proportion refed and laid a second batch with the technique employed. Oviposition was observed in *Aedes vexans* which laid about 1 to 2 eggs per minute. The eggs began darkening about 57 minutes after laying.

"CONDITIONING"

The normal procedure for hatching *Aedes* eggs is as follows. Eggs must be kept moist for several days after laying. If they are dried during the first few days (48 hours in *A. aegypti* [MacGregor,

1916]) they will be killed. After the embryo has developed to a certain point (which has not been fully elucidated) the egg becomes more resistant to drying. The egg can then be "conditioned" by exposing it to air for a few days; "conditioned" eggs hatch readily when placed in water to which a suitable "hatching stimulus" has been added.

The "conditioning" process is necessary for inducing uniform hatching. This was shown by an experiment in which 130 eggs of *Aedes trivittatus* were submerged in water immediately after laying. After 37 days only 15 had hatched. In another experiment involving *A. vexans* (from Minnesota) 2,350 eggs were submerged in tap water soon after laying. In a period of 9 days 269 larvae (12.7%) hatched. Batches of these eggs were transferred to bowls for further experiments and of 6 batches of 100 eggs, none hatched in 6 to 9 days. Neither ascorbic acid nor glutathione was effective in hatching these unconditioned eggs although exposure to a partial vacuum induced 44 of 100 to hatch.

These data and others not presented demonstrate that most eggs which have not been exposed to air ("conditioned") will not hatch, even in the presence of a hatching stimulus. This is true of *Psorophora longipalpis* as well as of the two species mentioned above.

THE EFFECT OF SUBMERSION OF EGGS IN WATER AFTER CONDITIONING

Eggs of *Aedes vexans, A. trivittatus, A. canadensis,* and *Psorophora longipalpis* were submerged in 5 cc. tapwater under the following conditions:

1. Water aerated (by bubbling air through it) a half hour before using.
2. Unaerated water.
3. Water boiled one quarter hour before using (exposed to air during experiment).
4. Water boiled one half hour before using (exposed to air during experiment).

Other groups of eggs were placed in different volumes (1, 2, or 3 cc.) of tapwater to test the effect of depth of the water. The results of these tests are given in table 1.

It can be seen that tapwater alone is not effective in inducing hatching of *Aedes* or *Psorophora* eggs. Eggs hatched in only two tests and then only 7 of 19. This point is illustrated further by an experiment on *Psorophora longipalpis* eggs. One hundred eighty-eight eggs of this species were submerged in distilled water imme-

TABLE 1.—The Effectiveness of Tapwater in Hatching Aedine Eggs.*

SPECIES	*A. vexans*	*A. trivittatus*		*A. canadensis*	*P. longipalpis*	
Time (days)†	1	1	5	1	1	5
aerated ½ hr.	0/10	0/10	0/10	0/5	0/10	0/10
unaerated	0/10	0/10	0/10	0/5	0/8	0/8
boiled ¼ hr.	0/10	0/10	0/10	0/5	0/9	0/9
boiled ½ hr.	0/10	.....	.....	.....	0/11	0/11
1 cc. volume	0/9	0/10	0/10	0/5	0/13	0/13
2 cc. volume	3/9	0/10	0/10	0/5	0/12	0/12
3 cc. volume	4/10	0/10	0/10	0/5	0/8	0/8

* The values given are the proportions which hatched; thus 0/10 is none of 10.
† Length of time after which the observation was made.

diately after laying. After 6 to 9 days none had hatched. They were then conditioned for 4 days, split into two parts and half were put into distilled water and half in "grass extract" (*vide infra*). In 24 hours 40 of 78 had hatched in the grass extract but none of 78 in distilled water.

If a hatching stimulant had been added to the batches of eggs tabulated in table 1, most of the eggs of *Aedes vexans, A. trivittatus,* and *Psorophora longipalpis* would probably have hatched. The eggs of *A. canadensis* would not have hatched (*vide infra*). These experiments actually served as controls for the experiments utilizing corn broth, grass extract, and urine which are discussed below.

PLANT MATERIALS AS HATCHING STIMULANTS

Since Horsfall (1956) has indicated that the broth from canned corn was effective in promoting hatching, a series of trials was made with this medium. A can of creamed corn * was opened and used as quickly as possible. The broth was filtered through cheesecloth and the filtrate diluted with tapwater to the concentrations given in table 2; the final volume in all cases was 5 cc.

From this table it can be seen that fresh "corn broth" is effective in hatching the eggs of *Aedes vexans, A. trivittatus,* and *Psorophora longipalpis* in concentrations as low as .05%. It appears that at the lower concentrations the time required for this response may be lengthened. These results fully confirm the results of similar experiments by Horsfall (1956).

It will be noticed that none of the eggs of *Aedes canadensis* hatched under these conditions. These eggs were all laid by a single female. In further experiments a very few eggs hatched,

* Del Monte cream style sweet corn.

demonstrating that the female had been inseminated. This species is commonly found only in the early spring and thus presumably has a single generation a year (although there are anomalous records). The results given above lend support to the idea that this form has an obligatory diapause in the egg stage.

TABLE 2.—The Effectiveness of Corn Broth in Hatching Aedine Eggs.*

SPECIES	*A. vexans*	*A. trivittatus*		*P. longipalpis*		*A. canadensis*
Time (days)...	1	1	5	1	5	1
Concentration: (percent)						
5.00.....	9/10	6/10	6/10	9/10	9/10	0/5
4.00.....	11/12	8/10	8/10	12/13	12/13	0/5
3.00.....	19/19	7/10	10/10	7/10	7/10	0/6
2.00.....	11/11	6/10	6/10	7/10	7/10	0/5
1.00.....	11/11	7/10	9/10	5/10	5/10	0/5
0.50.....	7/8	5/10	9/10	10/11	10/11	0/5
0.33.....	8/10	5/10	9/10	10/10	10/10	0/5
0.20.....	8/10	4/10	8/10	10/11	10/11	0/5
0.10.....	6/9	3/10	5/10	6/10	8/10	0/5
0.05.....	5/10	1/11	11/11	2/10	7/10	0/5
0.02.....	0/11	0/10	2/10	0/11	2/11	0/5

* The controls for these experiments are shown in table 1.

GRASS EXTRACT

There are many reports in the literature indicating that vegetation might promote the hatching of eggs. We therefore used extracts of grass (*Setaria glauca* [Linnaeus]) in hatching eggs. Approximately 200 cc. of loosely packed grass blades was macerated in 10 cc. tapwater and strained through cheesecloth. The filtrate was then diluted with tapwater to the appropriate concentration; the final volume was 5 cc. in all cases. The results of these tests are given in table 3; all readings were made after 24 hours.

As can be seen from the table, grass extract is also effective in promoting hatching of eggs of *Aedes trivittatus* and *Psorophora longipalpis*. In other tests not listed the same was found true for *A. vexans*, *A. triseriatus*, and *A. aegypti*. A single larva of *A. canadensis* hatched which shows the eggs of this species were fertile but most were not in a "hatchable" condition.

EFFECT OF ALFALFA PELLETS

Commercial rabbit pellets made of dried alfalfa are used in this laboratory for feeding mammals and mosquito larvae. A group of these was crushed and sieved through screen wire. Five grams of

TABLE 3.—The Effectiveness of Grass Extract in Hatching Aedine Eggs

SPECIES	*A. trivittatus*	*P. longipalpis*	*A. canadensis*
Concentration: (percent)			
100.0	.....	0/10	.....
5.0	10/10	5/10	0/5
4.0	7/10	5/10	1/5
3.0	7/10	3/10	0/5
2.0	7/10	1/10	0/5
1.0	8/10	2/10	0/5
0.5	7/10	1/10*	0/5

* An additional larva hatched after 3 days.

this material was macerated in tapwater and then strained through cheesecloth. This stock solution was diluted with tapwater to the appropriate concentration. Five cc. of the final concentration was used in each test and readings were taken after 24 hours. The results are given in table 4.

Alfalfa pellets also are effective in stimulating the hatching of aedine eggs although possibly to a lesser extent than fresh grass. Similar observations have been made with *Aedes aegypti* in this laboratory.

The foregoing tests indicate that a variety of plant materials are capable of inducing hatching of dormant eggs of many species of aedine mosquitoes.

TABLE 4.—The Effectiveness of Dried Alfalfa Pellets in Hatching Aedine Eggs

SPECIES	*A. vexans*	*A. trivittatus*	*P. longipalpis*
Concentration: (percent)			
5.00	3/10	0/10	1/10
4.00	6/10	0/10	1/10
3.00	8/10	0/10	0/10
2.00	9/10	6/10	3/10
1.00	4/10	7/10	2/10
.50	10/10	4/10	6/10
.33	10/10	3/10	3/10
.20	10/10	3/10	2/10
.10	9/10	0/10	6/10
.05	8/10	1/10	5/10
.02	0/10	1/10	0/10
.00	0/10	0/10	0/10

THE EFFECT OF REDUCED OXYGEN CONCENTRATION

The dissolved oxygen in water may be easily removed by exposure to a vacuum. This fact is utilized in some laboratories for producing larvae of uniform age. The method works well with *Aedes aegypti* in the experience of the authors.

Some of the control eggs from the experiments given above were tested for viability by exposure to a reduced oxygen concentration. The tubes were merely placed in a desiccator which was evacuated with a water aspirator. The equipment used was faulty but served the purpose although the amount of vacuum used could not be measured. This treatment appears to have no deleterious effects on mosquitoes. Of the eggs tested 63 of 78 *Psorophora longipalpis* hatched, 20 of 30 *Aedes trivittatus,* and 2 of 35 *A. canadensis.*

EFFECT OF REDUCING AGENTS

Since there are indications in the literature that substances which lower the oxidation-reduction potential of a medium are useful in promoting hatching of eggs (Gjullin, Hegarty, and Bollen, 1941), a series of reducing agents was tested. These were:

1. hydrogen.
2. metals: iron, copper, tin, and zinc.
3. other chemicals: ammonium iodide and oxalic acid.

Hydrogen was bubbled through the water containing eggs; the amount used was not measured nor was there a control to measure the effects of agitation although the gas was bubbled through the top of the water to reduce the effects of agitation. The other reagents were made up by using 25 to 500 mgm. in 5 cc. of distilled water which gave concentrations of 0.500 to 0.025% for the soluble compounds. The metals were in as finely divided a state as possible (filings or small particles). All tests were done with *Aedes vexans.*

Hydrogen was bubbled through water containing "conditioned" eggs and of the 30 eggs used (in three tests) 21 hatched within 15 minutes (5, 7, and 9 of the 10 in each test). Another group of 21 eggs was not "conditioned" but had been continuously submerged since laying (14 days); of 21 such eggs tested only one hatched. Since no catalyst was used in this experiment the hydrogen may have acted not by lowering the oxidation-reduction potential but by displacing a part of the oxygen in solution.

Of the metals tested neither tin nor copper induced hatching of eggs; zinc and iron, on the other hand, were effective (table 6) but the larvae were killed by exposure to zinc. Of the other materials tested ammonium iodide did not promote hatching; oxalic acid did

induce hatching (table 5) but killed the larvae when they were half out of their shells. There was no hatching in distilled water controls but satisfactory hatching in grass extract controls.

The reducing agents which were ineffective may have been too weak or may have killed the larvae before they were able to hatch. The former hypothesis is the more likely one but the viability of the unhatched eggs was not determined. A rusting iron pan was tested as a routine egg-hatcher and worked fairly well but slowly. Eggs did not hatch when placed in water in an aluminum pan.

TABLE 5.—Effectiveness of Reducing Agents in Hatching Eggs of *Aedes vexans*

REDUCING AGENT	Weight used (mgm.)	24 hrs.	48 hrs.	REDUCING AGENT	Weight used (mgm.)	24 hrs.	48 hrs.
Iron	25	8/10	8/10	Oxalic acid	25	3/10	.....
	50	4/10	8/10		50	0/10	.....
	100	6/10	8/10		100	5/10	.....
	500	5/10	5/10		500	7/10	.....
Zinc	25	1/10	4/10	Distilled water	.....	0/20	0/20
	50	5/10	5/10		.....	0/5	.....
	100	7/10	8/10	Grass extract	.....	16/30	18/30
	500	3/10	4/10		.....	4/6	.....

URINE

Since *Aedes vexans* larvae are frequently encountered in huge numbers in water fouled with urine and feces of cows, urine was tested as a possible stimulant. Male human urine was collected and diluted with tapwater to the desired concentration; the final

TABLE 6.—The Effectiveness of Urine in Hatching Aedine Eggs

SPECIES	*A. vexans*	*A. trivittatus*	*P. longipalpis**	*A. canadensis**
Concentration: (percent)				
10.0	.....	8/10	0/4	0/5
5.0	.....	8/10	9/9	0/5
4.0	.....	6/10	8/10	0/5
3.0	.....	6/10	7/10	0/5
2.0	.....	7/10	7/10	0/5
1.0	8/9	7/10	11/11	0/5
.5	9/11	2/10†	7/9	0/5
.1	7/11	4/10	7/10	1/5

* No additional larvae after 2 days.
† Seven additional larvae after 2 days.

volume was 5 cc. in all cases. Observations were made after 24 hours. The results of using this medium are shown in table 6.

These tests indicate that urine is effective in promoting hatching of eggs of *Aedes trivittatus, A. vexans,* and *Psorophora longipalpis* but not of *A. canadensis.* Tests were made of urea in concentrations of 5.00 to .02% to see whether or not it was the active ingredient of urine. No hatching occurred in these tests but they were inconclusive since there was poor hatching in the controls.

Aedes nigromaculis

A female laid 156 eggs on the surface of tapwater where they remained 13 days with none of the eggs hatching. During this time a scum developed on the water. After the above period the eggs were submerged in the water. Hatching began immediately. In 24 hours 139 of 156 had hatched and after 48 hours 141 of 156. The water used in this test developed a considerable amount of bacterial growth although no food had been added.

DISCUSSION

All evidence indicates that several steps are necessary for uniform hatching of eggs of multivoltine aedine mosquitoes.

1. The eggs must be in contact with free water while undergoing a certain amount of their development. This period has not been extensively studied but appears to be about 48 hours in *Aedes aegypti* (MacGregor 1916).

2. To become "hatchable" eggs must be "conditioned"; *i. e.,* exposed to air for a certain period of time. The duration of this period also has not been extensively investigated.

3. To hatch eggs it is necessary to use a "hatching stimulus" of some type. It appears likely that all of these stimulants lower the oxidation-reduction potential of the medium (Gjullin, Hegarty, and Bollen 1941).

In this study tests on *Aedes vexans, A. trivittatus, A. aegypti,* and *Psorophora longipalpis* indicated that the above steps are necessary for inducing hatching; one group of *Aedes nigromaculis* eggs reacted similarly. Horsfall (1955) has indicated that most multivoltine aedines correspond to this pattern. There are a large number of aedines, however, which appear to have a single generation a year and whose eggs will not hatch when put through the above regime. *Aedes canadensis* is probably one of these univoltine forms although there are anomalous findings in its behavior (large fall populations, for example, are frequently encountered). Our re-

sults with *canadensis* eggs confirm this hypothesis although the eggs were all derived from a single female.

The techniques described in this paper should be of value to culicidologists since larvae can be easily secured from biting females of most southern species of *Aedes* and *Psorophora*. This is useful in identifying questionable females and in securing larvae where none can be found in the field.

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A Revision of the Genus *Osmia*, Subgenus *Centrosmia* (Hymenoptera: Megachilidae)[1]

BY

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ABSTRACT: This paper consists of a taxonomic revision of the nine species of the subgenus *Centrosmia*. Keys to the species, detailed descriptions, and distributional data are given. The following new synonymy is indicated: *Osmia universitatis* Cockerell, *integrella* Cockerell, *amala* Cockerell, and *metitia* Cockerell are all synonyms of *O. pikei* Cockerell.

INTRODUCTION

This work is a taxonomic revision of bees of the subgenus *Centrosmia* Robertson of the genus *Osmia* Panzer. The name *Centrosmia* was proposed by Robertson (1903) for *Osmia bucephala* Cresson. Sandhouse (1939) placed it as a synonym for *Melanosmia* Schmiedeknecht. Sinha (1958) recognized *Centrosmia* as a distinct subgenus and listed eight more species, most of which Sandhouse had placed in *Nothosmia*. As here understood, therefore, the subgenus includes a section of the *Nothosmia* of Sandhouse's revision, as well as two species which she placed in *Melanosmia*.

Most species of this subgenus are easily distinguishable by the swollen second and third tarsal segments of the middle leg of the male and by a protuberance or ridge near the base of the mandible and a thickened apical truncation of the clypeus in the female. A full description of the subgeneric characters, in comparison to those of other subgenera, will be given in a forthcoming paper (Sinha, 1958). An adequate discussion of its relationships with other subgenera cannot be given here since it would involve groups (subgenera) which will not be named or defined until the appearance of the paper by Sinha already mentioned.

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Eight of the species of this subgenus are extremely scarce, and only a few dozen specimens of these species have been seen after examining approximately 25,000 specimens of *Osmia* collected from the United States and Canada. Specimens of the species *bucephala* are somewhat less scarce.

The greatest difficulty was encountered in the association of the sexes. Although both of the sexes of the type species, *bucephala*, and of its relative, *nigriventris*, were known, the seven other species were described from the male only. The present authors were able to recognize a female of *universitatis* (= *pikei*). This sex association was confirmed by comparing the common subgeneric characters with the female of *bucephala*. Now that the subgeneric characters of the female are better established, it will be easier to associate the females of the remaining species when they are collected.

Ocellocular, postocellar and ocelloccipital lines are measured from the center of each ocellus. The morphological terminology used in the descriptions is from Michener (1944). References to species in the catalogues and general treatments of Dalla Torre (1896), Cresson (1887), Friese (1911), and Michener (1951) have been omitted in the synonymies, as these are bibliographic treatments which list or describe all species described before their dates of publication, without addition of any new information.

It will be noted that the present paper contains no illustrations. This is because adequate illustrations for understanding the characters of the species of *Centrosmia* were presented by Sandhouse (1939), Michener (1957), and Sinha (1958).

The authors wish to thank Dr. Wallace E. LaBerge, formerly of the University of Kansas but now of Iowa State College, for his constructive criticism in the preparation of the manuscript, and Mr. Karl V. Krombein for allowing them to see the types and the collections of *Osmia* in the United States National Museum, Washington, D. C.

KEY TO THE SPECIES OF THE SUBGENUS CENTROSMIA

Males

1. Middle leg with tarsal segments 2 and 3 unmodified; metasomal tergum 6 with apical impunctate band poorly defined, narrow or absent, distinctly different from bands of preceding terga 2

   Middle leg with tarsal segments 2 and 3 swollen or otherwise modified, at least slightly broader than basitarsus; metasomal tergum 6 with apical impunctate band wide like that of preceding terga or tergal margin reflexed 3

2. (1) Entirely black; abdomen widest near posterior end; metasomal tergum 6 with apical portion strongly reflexed forming a flange, especially laterally ..... *nigriventris*

Body metallic bluegreen; abdomen widest near middle; metasomal tergum 6 not reflexed ..... *bakeri*

3. (1) Size large (length usually 10 mm. or more); abdomen widest near posterior end; metasomal tergum 6 with apical portion strongly reflexed forming a flange ..... *bucephala*

Size smaller (length usually less than 10 mm.); abdomen widest in the middle; metasomal tergum 6 with apical portion not or but little reflexed 4

4. (3) Last flagellar segment expanded and compressed; metasomal tergum 6 with a median basal tuft of long, posteriorly directed hairs; tergum 7 with greatly thickened lateral margins. *vandykei*

Last flagellar segment unmodified; metasomal tergum 6 lacking a median basal tuft of long, posteriorly directed hairs; tergum 7 with lateral margins little thickened 5

5. (4) Hind leg with basitarsus strongly expanded, greatest width about one third of length ..... *tanneri*

Hind leg with basitarsus not or little expanded, greatest width less than one third of length 6

6. (5) Metasomal tergum 7 with a sharply pointed tooth on each side of deep midapical emargination; clypeal margin with median third produced, apex of projection weakly emarginate. *austromaritima*

Metasomal tergum 7 with a blunt lobe on each side of shallow midapical emargination; clypeal margin without midapical projection 7

7. (6) Seventh tergum with emargination shallowly arcuate, margins of tergum lateral to teeth not strongly convex; first flagellar segment (on shortest side) distinctly shorter than second; sternum 4 with apex conspicuously truncate; sternum 6 having apical process with lateral margins diverging posteriorly, apex rounded ..... *pikei*

Seventh tergum with emargination deep, margins of tergum lateral to teeth strongly convex; first flagellar segment (on shortest side) scarcely shorter than second; sternum 4 with apex rounded or subtruncate; sternum 6 having apical process parallel sided or narrowing posteriorly, apex not rounded 8

8. (7) Emargination of sternum 3 very shallow, less than one sixth as wide as sternum, fringed with whitish hairs; sternum 4 broadly rounded; sternum 6 having apical process emarginate at tip ..... *thysanisca*

Emargination of sternum 3 deeper, nearly one fourth as wide as sternum, fringed with yellowish hairs; sternum 4 subtruncate; sternum 6 having apical process truncate ..... *raritatis*

Females

1. Second mandibular tooth nearly as large as the others so that the mandibles are clearly four-toothed; body entirely without metallic coloration ..... *nigriventris*
   Second mandibular tooth much smaller than adjacent teeth; body with at least some areas of metallic blue or green coloration 2
2. (1) Mandible with a protuberance at upper basal angle, without ridge at lower basal angle; malar space broad; hind tibia with spurs strongly curved near apices ..... *bucephala*
   Mandible without protuberance at upper basal angle, with transverse ridge near lower basal angle; malar space inconspicuous; hind tibia with spurs almost straight near apices ..... *pikei*

Osmia (*Centrosmia*) *bucephala* Cresson

Osmia bucephala Cresson, 1864, Proc. Ent. Soc. Philadelphia, vol. 3, p. 17; Cresson, 1875, Rep. U. S. Georgr. Surv. West of 100th Meridian, p. 724; Robertson, 1895, Trans. Amer. Ent. Soc., vol. 22, p. 125; Evans, 1896, Canadian Ent., vol. 28, p. 13; Friese, 1902, Fauna arctica, Bd. 2, p. 482; Lovell and Cockerell, 1907, Psyche, vol. 14, p. 17; Graenicher, 1910, Bull. Public Mus. City Milwaukee, vol. 1, p. 245; Cockerell, 1911, Canadian Ent., vol. 43, p. 391; Gibson, 1915, 46th Ann. Rep. Ent. Soc. Ontario, p. 30; Cresson, 1916, Mem. Amer. Ent. Soc., no. 1, p. 113; Sandhouse, 1925, Canadian Ent., vol. 57, p. 36; Leonard, 1926, Cornell Univ. Agr. Expt. Sta., Mem. 101, p. 1030; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 116, Beck, 1929, Bull. Brooklyn Ent. Soc., vol. 24, p. 304; Cockerell, 1934, Amer. Mus. Nov., no. 697, p. 13; Graenicher 1935, Ann. Ent. Soc. Amer., vol. 28, p. 305; Brimley, 1938, Insects of North Carolina, p. 458; Proctor, 1938, Biol. Surv. Mt. Desert Region, vol. 6, p. 445; Bohart, Knowlton, and Bailey, 1950, Utah State Agr. College, memeo. series no. 371 (female).

Osmia (*Centrosmia*) *bucephala,* Viereck, 1916, Connecticut Geol. and Nat. Hist. Surv., Bull. 22, p. 750.

Osmia (*Melanosmia*) *bucephala,* Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 37.

Osmia megacephala Cresson, 1864, Proc. Ent. Soc. Philadelphia, vol. 3, p. 18; Putnam, 1876, Proc. Davenport Acad. Nat. Sci., vol. 1, p. 195; Cresson, 1876, Proc. Davenport Acad. Nat. Sci., vol. 1, p. 209; Viereck, *in* Skinner, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 47; Cockerell, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 305; Cresson, 1916, Mem. Amer. Ent. Soc., no. 1, p. 123; Cockerell, 1919, Ent. News, vol. 30, p. 294; Clements and Long, 1923, Experimental Pollination, Carnegie Inst. Washington Publ. 336, p. 253; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 122; Cockerell, 1934, Amer. Mus. Nov., no. 697, p. 14 (female).

Osmia latitarsis Cresson, 1864, Proc. Ent. Soc. Philadelphia, vol. 3, p. 20; Cresson, 1878, Trans. Amer. Ent. Soc., vol. 7, p. 105; Provancher, 1888, Additions et Corrections av volume II de la Faune Entomologique du Canada, p. 327; Cresson, 1916, Mem. Amer. Ent. Soc., no. 1, p. 123 (male).

Osmia lignivora Packard, 1867, Amer. Nat., vol. 1, p. 376; Ashmead, 1894, Psyche, vol. 7, p. 39; Washburn, 1919, 17th Report State Entomologist Minnesota, p. 233; Cockerell, 1907, Univ. Colorado Studies, vol. 5, p. 37 (female).

Osmia lignicola Provancher, 1882, Nat. Canad., p. 208; Provancher, 1883, Faune Entomologique du Canada, Hyménoptères, p. 708 (female).

Osmia tarsata Provancher, 1888, Additions et Corrections au volume II de la Faune Entomologique du Canada, p. 328 (male).

Osmia subornata Cockerell, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, p. 342; Sandhouse, 1924, Proc. California Acad. Sci., ser. 4, vol. 13, p. 361, 370.

Centrosmia bucephala, Robertson, 1903, Trans. Amer. Ent. Soc., vol. 29, p. 170; Titus, 1906, Proc. Ent. Soc. Washington, vol. 7, p. 157; Robertson, 1928, Flowers and Insects, p. 8.

Centrosmia tarsata, Titus, 1906, Proc. Ent. Soc. Washington, vol. 7, p. 158.

This is the largest and most highly modified species of the subgenus. It has extensive black, nonmetallic areas, thus approaching *nigriventris* which is entirely black. The genal areas of the female are more than twice as wide as the eyes. This character alone distinguishes *bucephala* from all the other species of the subgenus. The male is unique in having the fourth as well as the second and third tarsal segments of the middle leg much enlarged and modified.

Male: Length of body, 12 to 14 mm. *Coloration:* Black with strong greenish blue tints on face and dorsum of head and thorax, more bluish on abdomen; lateral and ventral surfaces of head and thorax usually nonmetallic but sometimes bluish; mandible black; flagellum dark brown above and black below; legs black. *Pubescence:* Hair of body white, mixed with fuscous on vertex and genal area; on terga 3 to 5 black or largely so; fuscous or black hairs present on tibiae and basitarsi and sometimes replacing white; hair on undersides of tarsi golden. *Head:* Mandible with a narrow V-shaped notch separating short upper tooth from long slender, lower tooth, apical edge above notch convex, superior apical angle forming a right angle; carinae parallel, upper carina wider than lower, space between them narrow; facial length and width as 8:6.6; postocellar line shorter than ocelloccipital line and subequal to ocellocular; clypeus convex, apex weakly wavy, punctures finer than those on rest of face, apical impunctate band over one-third as wide medially as greatest width of scape; scape shorter than antennal segments 2 to 4 combined; length and width of eye as 7.5:3.3; eye nearly as wide as genal area; eyes with inner margins weakly converging to parallel; hypostomal carina moderately low, a little raised well behind angle. *Mesosoma:* Middle leg with tibial spine nearly twice as long as that on foreleg; strigilis with apex of velum convex, inner apical angle broadly rounded, apex of malus produced into a medium-sized, slender, spine that is about one sixth the length of rest of malus; foreleg with segments of mediotarsus broadened and flattened, second tarsal segment about as broad as long, third shorter, fourth still shorter; middle leg with segments of mediotarsus

greatly swollen, tarsal segments 2 to 4 as wide as or wider than long with inferior as well as lateral lobes, basitarsus twice as long as wide at its widest part; hind basitarsus narrowest at base, gradually widened towards apex; hind tibial spurs curved, inner much stouter than and nearly twice as long as outer. Forewing with length and breadth as 11:3.5, papillae on apex fine, moderately sparse, with hairs in cells short, sparse, dense in some areas. Propodeal triangle finely lined, shining below, dull and reticulate above. *Metasoma:* Terga 2 to 5 with apical impunctate bands one-fifth to one-third as wide as punctate portions, weakly lined, shining; tergum 5 with lateral margins reflexed; tergum 6 with long hairs laterally, apical margin reflexed, broadly convex with middle third subtruncate or gently concave; tergum 7 with long hair on sides bending mesad, surface convex, median emargination small and shallow. Sternum 1 with margin convex, usually with minute midapical emargination; sternum 2 with margin convex, most strongly so medially although sometimes with small shallow midapical emargination, a subtriangular or rounded tumescence at or just anterior to midapex which bears fuscous or black hairs directed mesad and caudad and contrasting with adjacent white hairs; sternum 3 with midapical concavity deep, wide, fringed with moderately long light golden hairs directed mesad; sternum 4 with margin broadly rounded, one fourth of posteromedian area covered by a nearly semicircular patch of coarse black bristles directed to the rear and mesad; sternum 5 with small V-shaped median emargination; sternum 6 with apical margin subtruncate laterally, median produced portion with sides parallel and apex emarginate on each side of broadly triangular middle portion; sternum 8 with apical half nearly truncate on each side of long, slender, median projection, basal half subtriangular. Gonocoxite broad at base with a ventral lobe at level of angle, with a few long bristles on mesal surface at point of divergence of this lobe, and a lateral patch of bristles on dorsal surface of angle; free portion of volsella blunt subconical; penis valve reaching beyond angle of gonocoxite, sides nearly parallel, apex slightly wider, tip broadly rounded.

Female: Length of body 13 to 16 mm. *Coloration:* Black, usually with face, thoracic dorsum, and metasomal terga weakly greenish blue. *Pubescence:* Hair on face, vertex and metasomal tergum 2 black mixed with white; on dorsum and sides of thorax (only a few isolated black hairs), propodeum, metasomal tergum 1 and sometimes anterior half of metasomal tergum 2 white; on under-

side of foretarsus golden brown (darker in some individuals); on lower surfaces of middle and hind tarsi dark reddish brown; on rest of body black. *Head:* Mandible with superior apical angle (tooth 1) acute, tooth 2 missing or represented by feeble convexity nearer tooth 3 than 1; length of triangular tooth 3 about one third length of sharp, slender, triangular tooth 4 (inferior apical angle of mandible); distance between teeth 1 and 3 over twice distance between 3 and 4; mandibular carinae parallel, lower carina wider than upper; carina on upper edge weakly wavy, slightly curving down apically near base of tooth 1; mandible with apex about one and one-third times as wide as constriction which is slightly narrower than base; a distinct protuberance, highest near upper basal angle of mandible, occupies nearly three fourths of basal width of mandible and sharply cuts off a narrow unmodified basal zone; labial palpus with segment 1 three-fourths as long as 2; maxillary palpus with segment 3 a little longer than 2 and nearly as long as 4 and 5 together; face as long as wide; postocellar line little over half as long as ocellocular line; ocelloccipital line two to two and one-half times as long as postocellar; clypeus strongly convex basally, with punctures equal to those on anterior half of paraocular area, coarser than those on rest of face, medially longitudinally keeled and closely and rather finely punctate, apex of truncation broadly and strongly thickened and elevated, irregularly coarsely punctate, with distance between lateral angle of apical truncation and lateral angle of clypeus shorter than length of apical truncation; eyes with inner margins diverging below, each a little less than three times as long as wide; base of mandible nearly twice as wide as eye; malar space longer than flagellar width; flagellum with segment 1 a little less than twice as long as pedicel; hypostomal carina moderately low, slightly raised a short distance behind angle. *Mesosoma:* Foreleg with tibial spine subequal to that of middle leg; longest hair on fore basitarsus half as long as basitarsus; strigilis with apex of velum oblique, merging into malus, malar spine one third as long as length of malus, inner apical angle of velum more nearly an obtuse angle than rounded, inner basal angle rounded and more pointed than inner apical angle; hind tibial spurs long, slender, strongly curved apically. Forewing with length and width as 11:3.5, with papillae on apex fine, sparse, with hair in cells short and dense with few longer and sparse hairs in some areas. Mesoscutum shining, punctures fine and confluent anteriorly and laterally, separate in large discal area. Propodeal triangle reticulate in narrow upper portion,

aciculate below. *Metasoma:* Punctures shallow and widely separated, impunctate bands on terga 2 to 5 at least one-fourth as wide as punctate portions, sixth tergum rather finely and closely punctate in contrast to preceding ones.

Type material: The holotype of *bucephala* is from Great Slave Lake, North West Territories, Canada; that of *megacephala* is from the Rocky Mountains in Colorado; and the lectotype of *latitarsis* is from New York; all of these are in the Academy of Natural Sciences of Philadelphia. The cotypes of *lignivora* from Lawrence, Massachusetts are in the Museum of Comparative Zoology, Cambridge, Massachusetts. The one labeled Type/1/540 is here designated the lectoholotype. The other, Type/2/540, becomes a lectoparatype. The types of *lignicola* and *tarsata,* both from Cap Rouge, Quebec, are in the Musée de la Province de Quebec. The holotype of *subornata* from Olympia, Washington, is in the United States National Museum.

Distribution: This species is widely distributed in North America, from coast to coast and Alaska and the North West Territories to New Mexico, North Carolina, and Oregon, limited to mountains in the southern part of the range. Specimens from the following localities have been examined:

ALASKA: Matanuska, July 17, 1944 (J. C. Chamberlin); White Horse to Yukon Crossing, May 15 to 20, 1912 (J. M. Jessup). YUKON TERRITORY: Deer Lake, White Pass, May 19, 1916 (J. A. Kusche). NORTHWEST TERRITORIES: Fort Resolution, Great Slave Lake, June 26, 1903, on *Taraxicum* (Mack). BRITISH COLUMBIA: Vancouver, June 14, 1902. ALBERTA: Bilby, June 25, 1924 (G. Salt); Edmonton, May 30, 1924 (G. Salt). ONTARIO: Merivale, May 12, 1930 (J. J. de Gryse). QUEBEC: Danford Lake, June 3, 1917 (F. W. L. Sladen). NOVA SCOTIA: Kings County, May 30, 1931 and June 5, 1932 (G. E. Atwood). WASHINGTON: Olympia, May 22 and 25, 1894; Pullman, June 7, 1905. OREGON: Mt. Hood, 3000-6000 feet, June 24, 1925 (E. C. Van Dyke); Pamelia Lake, Mt. Jefferson, July 15, 1907 (J. C. Bradley); Steens Mountains (west side, above 8000 feet) July 12, 1927 (H. A. Scullen). IDAHO: Franklin, June 1, 1948 (G. E. Bohart). UTAH: Curran Creek Valley, Uinta National Forest, 8000 feet altitude, July 4, 1917 (J. Silber); North Fork of Duchesne River, July 13 to 14, 1927; Monte Cristo, July 3, 1950 (G. F. Knowlton and S. L. Wood); La Sal Mountains, Mt. Tukuhni-

kivatz (V. M. Tanner). Montana: Lake St. Marys, Glacier National Park, June 1, 1938 (E. C. Van Dyke). Colorado: Elk Creek, Fraser, Grand County, July 7, 1927 (J. C. Bradley), Ute Creek, 9000 feet altitude, July (H. S. Smith); Russell, June 25, 1907 (L. Bruner); Science Lodge, west Boulder County, June 24, 1938 (Helen Rodeck), July 8, 1936 (Helen Rodeck, U. Lanham), July 22-23, 1922 (L. O. Jackson); Zimmermans, August 26, 1935 (Figgins); Creede, 8844 feet altitude, August, 1914 (S. J. Hunter); Sargent, June 21, 1926 (E. G. Anderson); South Fork, Rio Grande, 37° 36′ N, 106° 43′ W., 8500 feet altitude, June 17, 1919. Iowa: Ames, May 6, 1897, at violet (E. D. Ball). Indiana: Elkhart. New York: Keeseville, June 2, 1918 (A. K. Fisher); Ithaca (Chittenden); Axton, June 12 to 22, 1901. Maine: Old Orchard, June 6, 1921 (T. B. Mitchell). Massachusetts: Amherst, June 27, 1904. Connecticut: Hartford, May 7, 1899. Pennsylvania: Linglestown, June 26, 1917 (W. S. Fisher). Maryland: near Plummers Island, April 25 and 28, 1915, May 3, 1916, on *Mertensia virginica* and *Nepeta hederacea* (J. C. Crawford). North Carolina: Durham, May 4, 1904 (J. R. Randall); Bryson City, June 8, 1923, on *Tephrosia virginiana* (J. C. Crawford); Cruso, June 28, 1934; Smokemount, June 30, 1934. The species has also been recorded from New Hampshire, Virginia, Tennessee, Illinois, and New Mexico.

As Sandhouse (1939) has pointed out, there is a general tendency for western specimens to have more black pubescence than eastern ones and perhaps also less metallic coloration on the body surface. Thus females from the Appalachian region to Great Slave Lake usually have the mesoscutal pubescence entirely pale or nearly so, those from Colorado have a considerable area of mixed pubescence on the mesoscutum, while those from Washington state usually have a discal area of largely black pubescence and also have the pubescence of the face and vertex largely black. Males show similar tendencies. For example, the hair of the third to fifth terga is mixed black and white in the east, nearly all black from Colorado westward. The differences are probably sufficient to justify recognition of two subspecies, *O. bucephala bucephala* Cresson for the subarctic and eastern area and *O. bucephala megacephala* Cresson for the montane western area, but as adequate series for a study of variation in any one locality are not available, formal recognition seems premature and is not necessary in any event.

Osmia (*Centrosmia*) *nigriventris* (Zetterstedt)

Anthophora nigriventris Zetterstedt, 1838, Insecta Lapponica Descripta, vol. 1 p. 465.

Osmia nigriventris, Nylander, 1848, Notiser ur Sällsk Fauna Fennica Förh., vol. 1, p. 260.

Osmia (*Melanosmia*) *nigriventris*, Schmiedeknecht, 1884-86, Apidae Europaeae, vol. 2, p. 79; Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 35.

Osmia corticalis Gerstaecker, 1886, Stettiner Ent. Zeitung, vol. 30, p. 331.

Osmia frigida Smith, 1853, Catalogue of Hymenopterous Insects in the Collection of the British Museum, pt. 1, p. 142; Cresson, 1864, Proc. Ent. Soc. Philadelphia, vol. 3, p. 26; Evans, 1896, Canadian Ent., vol. 28, p. 13; Friese, 1902, Fauna Arctica, vol. 2, p. 483; Cockerell, 1905, Trans. Amer. Ent. Soc., vol. 31, p. 332. Sandhouse, 1925, Canadian Ent., vol. 57, pp. 36, 65. (Provancher's [1883] records of this species relate to *Megachile* according to Titus, 1905).

Osmia hudsonica Cresson, 1864, Proc. Ent. Soc. Philadelphia vol. 3, p. 21; Friese, 1902, Fauna Arctica, vol. 2, p. 483; Gibson, 1916, 47th. Ann. Rep. Ent. Soc. Ontario, p. 26; Cresson, 1916, Mem. Amer. Ent. Soc., no. 1, p. 120.

In the above synonymy, no effort has been made to include references to all European citations of the species; only original descriptions and new combinations have been cited. This is the only wholly black, nonmetallic species of *Centrosmia*. In this respect it resembles only one other American *Osmia*, *O. inermis* (Zetterstedt), which is morphologically like the group included by Sandhouse (1939) in *Nothosmia*. *O. nigriventris* shows evidence of relationship with *bucephala*, e. g., the male hind basitarsus tapering toward the base, the enormous inner hind tibial spur of the male, the reflexed lateral margins of the fifth tergum and lateral and posterior margins of the sixth, in the male, etc. The unmodified middle tarsi of the male and the presence of a weak transverse ridge rather than a large protuberance at the base of the mandible of the female distinguish this species immediately from *bucephala*.

Male: Length of body, 11 mm. *Coloration:* Black, flagellum, tegulae, legs, and margins of metasomal segments brownish. *Pubescence:* White, light fuscous on second and following metasomal segments and outer sides of tibiae, yellowish on under sides of tarsi. *Head:* Mandible with small narrow V-shaped notch separating short upper tooth from longer lower tooth, apical edge above notch convex, superior apical angle feebly acute; carinae subparallel, subequal in width, space between them narrow; facial length and width as 6:4; postocellar line shorter than ocelloccipital line and subequal to ocellocular; clypeus convex, apex wavy, punctures fine and very dense like those of supraclypeal area and lower part of paraocular area, apical impunctate band nearly two-thirds as wide as greatest

width of scape; eye nearly as wide as genal area; inner margins of eyes strongly converging below; hypostomal carina low, a little raised behind angle. *Mesosoma:* Middle leg with tibial spine smaller than that of foreleg; strigilis with apex of velum subtruncate, inner apical angle broadly rounded, apex of malus produced to a medium sized spine about one-sixth as long as entire malus; foreleg with segments of mediotarsus slightly broadened, second and third tarsal segments slightly longer than broad; middle leg with mediotarsus unmodified, second and third tarsal segments much longer than broad, basitarsus over four times as long as wide; hind basitarsus narrowest at base, gradually widened toward parallel sided apical region; hind tibial spurs curved, inner much stouter than outer and about 1.3 times as long as outer. Forewing with length and breadth as 3:1, papillae on apex very fine, moderately sparse, hairs in cells short, dense. Propodeal triangle dull and minutely granular, weakly striate along upper margin. *Metasoma:* Terga 2 to 5 with apical impunctate shining bands one fifth to one third as wide as punctate portions; tergum 6 with apical margin reflexed, broadly so laterally, margin broadly convex except for small shallow median emargination; tergum 7 with shallow median emargination, somewhat as in *pikei.* Sterna 1 and 2 with margins broadly convex; sternum 3 with midapical concavity deep, about one-third as wide as sternum; sternum 4 with margin broadly rounded, posterior median area covered by patch of coarse hairs directed to rear, this patch divided by longitudinal median depressed hairless line; sternum 5 with shallow median emargination; sternum 6 with apical margin truncate except for median produced portion which is parallel sided, the apex with lateral angles broadly rounded, middle feebly emarginate; sternum 8 with apical projection broadly subtriangular. Gonocoxite broad at base, with dense patches of inner, outer, and ventral bristles at and just distal to angle; free portion of volsella broadly rounded.

Female: Length of body 11 to 12 mm. *Coloration:* Black with flagellum, tegula, legs, and margins of metasomal segments slightly brownish. *Pubescence:* Hair of head and thorax white with yellowish to light fuscous hairs intermixed on clypeus, vertex, genal and hypostomal areas; tibiae and tarsi with hairs fuscous, rest of legs with white hairs or with fuscous intermixed on hind femora; first metasomal tergum and sides of second with white hair, sixth tergum with short white or light fuscous hair; rest of metasoma with hair black or dark fuscous, sometimes with white intermixed

on terga. *Head:* Mandible with superior apical angle (tooth 1) rounded acute, tooth 2 nearly as large as adjacent teeth; tooth 3 not much shorter than 4 which is short and triangular; teeth evenly spaced; mandibular carinae parallel, lower carina slightly wider than upper; carina on upper edge nearly straight, very slightly curved down apically near base of tooth 1, mandible with apex only slightly wider than constriction which is scarcely narrower than base; base of mandible abruptly depressed so that there appears to be a rounded transverse ridge across the mandible near the base, just distad of the depressed zone (this much as in *pikei,* but in that species lower part of ridge is elevated); labial palpus with segment 1 five-sevenths as long as 2; maxillary palpus with segment 3 longer than 2 and slightly longer than 4 and 5 together; face about as long as broad; postocellar line about three-fourths as long as ocellocular, the latter about equal to ocelloccipital line; clypeus convex with punctures over most of surface finer and denser than on anterior half of paraocular area and not much if any coarser than those of rest of face, truncation broadly and strongly elevated, slightly convex so that it is ill defined, anterior portion of thickened region smooth, posterior portion strigose punctate, distance between lateral angle of truncation and lateral angle of clypeus about equal to length of truncation; eyes with inner margins converging below, each three times as long as wide; base of mandible wider than eye; flagellum with segment 1 one and one-third times as long as pedicel; hypostomal carina moderately low, slightly raised a short distance behind angle. *Mesosoma:* Foreleg with tibial spine about half as long as that of middle leg; longest hair on fore basitarsus over half length of basitarsus; strigilis with apex of velum oblique, merging into malus, malar spine one-fourth as long as entire length of malus; inner apical angle of velum broadly rounded, inner basal angle rounded but sharper than inner apical angle; hind tibial spurs long, slender, slightly curved apically. Forewing with length and width as 14.5:5, papillae on apex moderately fine, hair in cells short and dense. Mesoscutum rather dull, punctures nearly confluent anteriorly and laterally, separate in discal area. Propodeal triangle completely dull and granular, upper margin finely rugulose. *Metasoma:* Punctures shallow, largely separated by a puncture width or less, impunctate bands on terga 2 to 5 aciculate, one-third to one-sixth as wide as punctate portions; sixth tergum rather finely and closely punctate in contrast to preceding ones.

Type material: The type of *frigida* from "Hudson's Bay" is pre-

sumably in the British Museum (Natural History), of *hudsonica* from "Hudson's Bay Territory" is in the Academy of Natural Sciences of Philadelphia.

Distribution: Northern Europe, the Alps. In America, Alaska, Washington and Oregon to Hudson Bay and Ontario. Sandhouse records the species from Alberta, Montana, and Colorado in addition to the areas mentioned. Specimens before us are from Emigrant Gulch, Montana, May 12, 1919 (R. Kellog).

Osmia (Centrosmia) bakeri Sandhouse

Osmia bakeri Sandhouse, 1924, Proc. California Acad. Sci., ser. 4, vol. 13, p. 345 (male).

Osmia (Nothosmia) bakeri, Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 87.

This species differs from others of the subgenus *Centrosmia* in the unmodified midtarsal segments on the fore and middle legs combined with metallic blue coloration. It is close to *vandykei* in the general pattern of the genitalia, the strigilis, the clypeal margin, and the emargination of the sixth metasomal tergum, but differs from the latter in having unmodified flagellar segments and in lacking stiff black hairs on the sixth and seventh metasomal terga.

Male: Length of body 7 to 9 mm. *Coloration:* Dorsum of thorax, face and vertex of head greenish blue, pleura and abdomen dark blue; mandible black; flagellum usually lighter below than above; legs black except for weakly metallic femora. *Pubescence:* White, that of fourth and following sterna and lower surfaces of tarsal segments reddish brown. *Head:* Mandible with a wide, deep, V-shaped notch separating upper tooth from only slightly longer lower tooth; margin above notch oblique, unmodified; superior apical angle acute; mandibular carinae subparallel, converging at base of lower tooth, lower carina twice as wide as upper, space between them narrow; labial palpus with segments 1 and 2 as 5:8; maxillary palpus with lengths of segments 2 to 5 as 3:4:2:1; length and width of face at 6:5; postocellar line nearly equal to or slightly longer than ocellocular line; ocelloccipital line shorter than postocellar; clypeus convex, apex truncate, a little swollen, sometimes with shallow emargination and midapical triangular projection, with punctures finer than those of surrounding areas, with apical impunctate band about one-third as wide medially as greatest width of scape; scape as long as antennal segments 2 to 4 combined; pedicel half as long as first flagellar segment; last flagellar segment slightly longer than a typical segment, unmodified; length and width

of eye as 5.6:2.7; inner margins of eyes distinctly converging below; width of genal area nearly equal to eye width; hypostomal carina low, slightly raised behind angle. *Mesosoma:* Foreleg with tibial spine shorter than that of middle leg; strigilis with apex of velum truncate, apex of malus produced straight distad into a short, sharp spine, length of spine about one-eleventh of length of malus, inner apical angle of velum rounded, inner basal angle more broadly so, base of velum more than half as wide as malus; foreleg with segments of mediotarsus not swollen, tarsal segment 2 much longer than wide, third and fourth progressively shorter, basitarsus three times as long as wide; middle leg with coxa unmodified, mediotarsal segments not swollen, longer than wide, basitarsus five times as long as wide; hind basitarsus gradually narrowing towards base and apex, maximum width in middle, apex truncate; tibial spurs slender, almost straight apically. Forewing three times as long as wide, with papillae on apex fine, thick, with hair in cells short and dense. Propodeal triangle reticulate above, aciculate below. *Metasoma:* Terga 2 to 5 with apical impunctate bands about a fourth as wide as punctate portion; tergum 6 with or without wide, shallow undefined emargination; tergum 7 with produced portion gently emarginate and one-third as wide as apical margin, lateral tooth as wide as or wider than emargination and subtruncate. Sternum 1 with apical margin subtruncate; sternum 2 with slight swelling at midapex, apical margin broadly rounded, a fringe of lateral subapical, light yellow hairs; sternum 3 with midapical concavity shallow, only about one-fifth as wide as sternum, fringed with moderately long yellowish hairs directed posteriorly, such hairs continuing anteriorly as a median ventral stripe; sternum 4 with apical margin produced, strongly convex, middle third beset with short, rather sparse hairs, terminating in a fimbria of longer reddish brown hairs; sternum 6 with apical margin weakly convex with narrow, median, apically subtruncate projection beset with irregularly arranged short hairs; sternum 8 subtriangular with slender median apical process. Terminalia similar to those of most other members of subgenus *Centrosmia,* especially *vandykei,* but slender apical portion of gonocoxite shorter and hairs lateral to apical portion shorter; penis valve more strongly curved than *vandykei.*

Type material: Holotype male and two paratype males collected by C. F. Baker at Claremont, California; two paratype males collected by E. P. Van Duzee at Keen Camp, San Jacinto Mountains, Riverside County, California, June 6-12, 1917. The holotype is in

the collections of U. S. National Museum, Washington, D. C. (U. S. N. M. type no. 28117).

Distribution: West coast states from Washington to California. In addition to the type material, specimens from the following localities have been examined by the authors:

CALIFORNIA: Tetleys Mountain Camp, San Bernardino Mountains, May 16 (C. D. Michener); Marsh Creek Springs, Contra Costa County, April 24, 1937 (G. Ferguson); Huntington Lake, Fresno County, July 3, 1917 (I. McCracken). OREGON: Steens Mountains, 7000 feet altitude, July 10, 1927 (H. A. Scullen). WASHINGTON: Pullman, May 14, 1904 (A. L. Melander).

Osmia (Centrosmia) tanneri Sandhouse

Osmia tanneri Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 87.

This species resembles *pikei* in the shape of the sixth metasomal sternum and the genitalia but can be easily distinguished by the compressed and expanded hind basitarsus and the deep U-shaped emargination of the third sternum. This species is known from a single male; hence certain details which were not studied are omitted from the description. The female is unknown.

Male: Length of body 11 mm. *Coloration:* Face and dorsum of thorax dark blue, rest of body blue and greenish blue. *Pubescence:* Hair on face, vertex, hypostomal area, dorsum of thorax, base of posterior surface of forefemur, and middle of first metasomal tergum, white; on inner surface of tarsi dark brown; remainder black or mostly so. *Head:* Mandible with a wide, V-shaped notch separating slightly acute upper tooth from longer and narrower lower tooth; margin above notch oblique; mandibular carinae subparallel; postocellar, ocellocular and ocelloccipital lines almost equal to one another; clypeus convex; apical impunctate band narrow; scape as long as antennal segments 2 to 4 combined; flagellar segments 2 to 11 each nearly twice as long as wide, unmodified; eye more than twice as long as wide, slightly narrower than genal area; inner margins of eyes converging anteriorly; hypostomal carina low and uniform. *Mesosoma:* Strigilis with apex of velum oblique, apex of malus produced into spine, inner apical angle of velum broadly rounded. Foreleg with segments of mediotarsus not swollen, tarsal segment 2 longer than wide, basitarsus compressed, two and one-half times as long as wide; middle leg with coxa unmodified, mediotarsal segments greatly swollen, tarsal segments 2

and 3 wider than long; hind basitarsus flattened and expanded, little over twice as long as wide, widest distal of base, gradually narrowed towards apex which is obliquely subtruncate. Forewing with distal portion densely papillate, hairs on cells short and moderately sparse. Propodeal triangle with irregular ridges on upper third, aciculate below. *Metasoma:* Terga 2-5 with apical impunctate bands wide; tergum 6 with very weak median emargination; tergum 7 with deep midapical emargination of produced portion forming lobe on each side. Sternum 1 with apical margin weakly convex; sternum 2 with weak and narrow emargination on middle of moderately convex apical margin; sternum 3 with deep U-shaped median emargination, fringed with fine golden yellow hair; sternum 4 with median third produced, apex emarginate, with patch of posteriorly directed black hairs; sternum 5 with apical margin subtruncate; sternum 6 with narrow, median subtruncate produced portion with patch of hairs; sternum 8 triangular at base, truncate at apex except for slender median process. Gonocoxite lacking hairs on mesal margin, having a tuft of anterolaterally directed hairs on bulging ventrolateral surface of angle; penis valve curved mesally near apex; volsella triangular at free posterior end.

Type material: The unique specimen was obtained at Rosevere Creek, Raft River Mountains, Utah, by Vasco M. Tanner (U. S. National Museum type no. 52875) in June, 1928.

Osmia (*Centrosmia*) *thysanisca* Michener

Osmia thysanisca Michener, 1957, Jour. Kansas Ent. Soc., vol. 30, p. 39.
Osmia integrella, Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, pp. 84-85 (male).

Males of this species resemble *pikei* but are easily distinguished by the small, shallow emargination of the third sternum, the rounded apex of the fourth sternum, the emarginate apex of the process of the sixth sternum, and the relatively broad hind basitarsus. Females of *O. thysanisca* are unknown.

Male: Length of body 9 to 10 mm. *Coloration:* Blue, face and dorsum of head and thorax often greenish; mandible black, base nonmetallic; flagellum brown; legs dark brown, fore and hind femora weakly metallic. *Pubescence:* Hair on face, hypostomal area, vertex, dorsum of thorax, and most of first metasomal tergum, white; on genal area, pleuron, second (and often third) metasomal tergum and undersides of fore and middle femora white, often mixed with black; midapical emargination of metasomal sternum 3 with

pale and short hairs extending forward as band to base of sternum; inner surfaces of all tarsal segments with tawny or reddish hair; hairs elsewhere black. *Head:* Mandible with wide V-shaped notch separating upper tooth from slightly longer lower tooth; upper tooth with acute angle at apex, margin above notch oblique; mandibular carinae parallel throughout most of their lengths but converging at base of lower tooth; carinae subequal in width, space between them narrow; facial length and width as 6:5; inner margins of eyes distinctly converging anteriorly; labial palpus with lengths of segments 1 and 2 as 7:10; maxillary palpus with lengths of segments 2 to 5 as 8:11:6:4, postocellar and ocellocular lines equal, ocelloccipital line about two-thirds as long as postocellar line; clypeus convex, apical margin weakly wavy, punctures finer than those on surrounding areas, extremely dense, apical impunctate band one-third as wide as greatest width of scape; scape slightly shorter than antennal segments 2 to 4 combined; eye with length and width as 5.5:2.5; pedicel half as long as first flagellar segment; flagellar segment 1 almost as long as second; last segment slightly longer than a typical segment, unmodified; hypostomal carina moderately high, uniform; eye about as wide as genal area. *Mesosoma:* Foreleg with tibial spine slightly longer than that of middle leg; strigilis with apex of malus produced into a short, sharp, slender spine, length of spine about one-seventh the length of whole malus (spine included); velum with inner basal and apical angles smoothly rounded; segments of mediotarsus slightly swollen; tarsal segment 2 a little longer than wide; segments 3 and 4 progressively shorter and narrower; basitarsus nearly four times as long as wide; middle leg with coxa unmodified, mediotarsal segments much swollen, tarsal segment 2 slightly longer than wide, 3 wider than long, with anterior margin bulging and rounded, fourth unmodified; hind basitarsus widest slightly basal to middle, gradually narrowed towards ends, apex truncate; hind tibial spurs slender and weakly curved at apices, inner one much longer and stouter than outer. Forewing about three times as long as wide, papillae on apex fine, sparse, cells with hairs short, moderately sparse. Propodeal triangle wrinkled above, aciculate below. *Metasoma:* Terga 2 to 5 with apical impunctate bands about one-fourth as wide as punctate portions, shining; tergum 6 lacking median emargination, with apical margin not reflexed, broadly impunctate like preceding terga; tergum 7 with midapical emargination of produced portion moderately deep, forming a broad, angular lobe on each side of emargination. Metasomal

sternum 1 with apex broadly rounded, without midapical emargination; sternum 2 with apex more broadly rounded, with irregular long hairs along apical margin; sternum 3 with midapical concavity very shallow, about one-sixth as wide as sternum, fringed with fine whitish hairs, margin of sternum to each side of concavity with darker hairs; sternum 4 with large medial patch of black, posteriorly directed hairs, apical margin broadly rounded; sternum 5 with apical margin subtruncate; sternum 6 with median produced portion narrow, with cordate patch of bristles, apex of projection arcuate-emarginate; sternum 8 narrowly triangular basally, subtruncate apically with a long, slender, parallel-sided, median process. Genitalia similar to those of *pikei*.

Type material: Holotype male from Wildhorse Canyon, Steens Mountains, Oregon, 4270-6000 feet altitude, July 5, 1927 (H. A. Scullen) is in the collection of the United States National Museum.

Distribution: Oregon and Wyoming. Specimens from the following localities (in addition to the type locality) have been examined:

OREGON: Fish Lake, Steens Mountains, 7000 feet altitude, July 11, 1927; White Branch Meadow, Three Sisters, Frog Camp, 5500 feet altitude. WYOMING: Jackson Hole, June 20, 1936.

Osmia (*Centrosmia*) *raritatis* Michener

Osmia raritatis Michener, 1957, Jour. Kansas Ent. Soc., vol. 30, p. 40.
Osmia (*Nothosmia*) *universitatis*, Sandhouse, 1939, Mem. Ent. Soc. Washington, 1:84 (part).

This species is intermediate in its main characters between *pikei* and *thysanisca*. Thus the apex of the fourth sternum is neither conspicuously rounded as in *thysanisca* nor truncate as in *pikei*, but subtruncate; the emargination of the third sternum is much larger than in *thysanisca* but smaller than in *pikei*. The process of the sixth sternum is narrow and parallel sided, with the apex truncate, more as in *tanneri* than in any other species. The hind basitarsi are slightly broadened but not so much so as in *tanneri*. Females of *O. raritatis* are unknown.

Male: Body length 8 mm. *Coloration:* Blue, face and dorsum of head and thorax greenish; mandible black, base nonmetallic; flagellum dark brown; legs dark brown, femora with weakly metallic areas. *Pubescence:* Hair on face, hypostomal area, vertex, dorsum of thorax, mesepisterna, and first metasomal tergum, coxae, trochanters, tibiae, and outer sides of tarsi, white; on genal areas, and femora white with intermixed fuscous hairs; on second and

following metasomal terga mixed black and white, black predominating posteriorly; on metasomal venter fuscous except for yellowish white fringe of third sternum and pale short hairs anterior to this fringe. *Head:* Mandible with wide V-shaped notch separating upper tooth from slightly longer lower tooth; upper tooth with acute angle at apex, margin above notch oblique; mandibular carinae subequal in width, space between them moderate, carinae converging toward base of lower tooth. Facial length and width as 6:5; inner margins of eyes distinctly converging anteriorly; postocellar and ocellocular lines equal, ocelloccipital line about two-thirds as long as postocellar line; clypeus convex, apical margin wavy, punctures finer than those on surrounding areas, extremely dense, apical impunctate band one-half as wide as greatest width of scape; scape slightly shorter than antennal segments 2 to 4 combined; eye with length and width as 5.5:2.4; pedicel half as long as first flagellar segment; flagellar segment 1 almost as long as 2; last segment slightly longer than a typical segment; unmodified; hypostomal carinae moderately high, uniform; eye about as wide as genal area. *Mesosoma:* Foreleg with tibial spine longer than that of middle leg; strigilis with apex of malus produced into robust sharp spine, length of spine about one-seventh that of whole malus (spine included); velum with inner basal and apical angles rounded; segments of mediotarsus slightly swollen, tarsal segment 2 longer than wide, 2 and 4 progressively shorter and narrower; basitarsus nearly four times as long as wide; middle leg with coxa unmodified, mediotarsal segments much swollen, tarsal segment 2 slightly longer than wide, 3 wider than long with anterior margin bulging and rounded, 4 unmodified; hind basitarsus widest at basal third, gradually narrowed toward apex (sometimes nearly parallel sided), apex truncate; hind tibial spurs slender, weakly curved at apices, inner one longer and stouter than outer. Forewing about three times as long as wide, papillae on apex fine, sparse, cells with hairs short, moderately sparse. Propodeal triangle weakly wrinkled above, aciculate below. Terga 2 to 5 with apical impunctate bands about one-fourth as wide as punctate portions, shining; tergum 6 lacking median emargination, with apical margin not reflexed, nearly as broadly impunctate as preceding terga; tergum 7 with midapical emargination of produced portion moderately deep, forming a broad, angular lobe on each side of emargination. Metasomal sternum 1 with apex broadly rounded, without midapical emargination; sternum 2 with apex more broadly rounded with irregular

long hairs along apical margin; sternum 3 with midapical rather shallow concavity less than one-fourth as wide as sternum, fringed with yellowish hairs, margin of sternum on each side of concavity with long dark hairs; sternum 4 with large medial area of posteriorly directed hairs, apical margin subtruncate; sternum 5 with apical margin subtruncate; sternum 6 with median process narrow, parallel-sided, apex truncate; sternum 8 narrowly triangular basally, subtruncate apically except for long, slender, median process. Genitalia similar to those of *pikei*.

Type material: Holotype male, from Camp Creek Ranger Station, Colorado, 8700 feet altitude, 41° 0′ N, 106° 12′ W, June 19, 1920, is in the U. S. National Museum.

Distribution: Colorado, Washington, and California. Specimens from the following localities (in addition to the type locality) have been studied:

WASHINGTON: Selah, May 4, 1919 (H. A. Scullen). CALIFORNIA: Myers, 6300 feet altitude, June 9, 1930.

Osmia (*Centrosmia*) *pikei* Cockerell

Osmia pikei Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 19, p. 367; Cockerell, 1907, Univ. Colorado Studies vol. 4, p. 252; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 124; Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 94; Bohart, Knowlton, and Bailey, 1950, Utah State Agr. College, Mimeographed series, no. 371 (female).

Osmia universitatis Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 19, p. 538, vol. 20, p. 125; Cockerell, 1909, Canadian Ent., vol. 41, p. 131; Sandhouse, 1924, Proc. California Acad. Sci., ser. 4, vol. 13, pp. 358, 369; Sandhouse, 1925, Canadian Ent., vol. 57, pp. 36, 63; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 119; Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 84; Michener, 1957, Jour. Kansas Ent. Soc., (in press) (male) (new synonymy).

Osmia integrella Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 20, p. 124; Cockerell, 1909, Canadian Ent., vol. 41, p. 131; ?Sandhouse, 1925, Canadian Ent., vol. 57, pp. 36, 63; Cockerell, 1928, Univ. Colorado Studies, vol. 16, p. 119 (male) (new synonymy).

Osmia amala Cockerell, 1907, Ann. Mag. Nat. Hist., ser. 7, vol. 20, p. 447; Cockerell, 1909, Canadian Ent., vol. 41, p. 131; Cockerell, 1910, Canadian Ent., vol. 42, p. 312; Cockerell, 1928, Univ. Colorado Stud., vol. 16, p. 119 (male) (new synonymy).

Osmia metitia Cockerell, 1909, Canadian Ent., vol. 41, p. 130; Cockerell, 1928, Univ. Colorado Stud., vol. 16, p. 119 (male) (new synonymy).

Males resemble *thysanisca* and *raritatis* Cockerell but differ from both in the shallowly arcuate median emargination in the seventh metasomal tergum, a deeper emargination of the third sternum, a medially truncate and fimbriate apical margin of the fourth sternum, an apically convex median process of the sixth sternum and the shorter first flagellar segment in comparison to the second. The

female is easily distinguished from *bucephala* Cresson by smaller size, relatively smaller head, the nature of the tumescenses of the apical margin of the clypeus and the bases of the mandibles, the deep and confluent punctures on the vertex, the longer and sinuate upper mandibular carina, the slender segments of the middle tarsus, and the more uniformly metallic coloration.

Male: Length of body, 8 to 10 mm. *Coloration:* Dark blue, face, vertex and dorsum of thorax often greenish; mandible black, base nonmetallic, flagellum dark brown; legs dark brown or black. *Pubescence:* Hairs on face, hypostomal area medially, dorsum of thorax, most of pleuron, propodeum (except lateral black patches), and metasomal tergum 1 white; on metapleuron, posterior femur and metasomal terga 4 to 7 and second and following sterna, black, on lower surfaces of middle and hind tarsi dark brown to black towards proximal ends; elsewhere black with few white mixed, or hairs of legs and genal areas all black (one specimen has hairs of legs nearly all pale). *Head:* Mandible with a wide, deep, V-shaped notch separating upper tooth from long, narrow lower tooth; apical edge above notch oblique, unmodified; superior apical angle acute; mandibular carinae parallel, lower carina slightly wider than upper, space between them narrow; labial palpus with segment 1 equal to segment 2; maxillary palpus with segment 2 subequal to length of segments 4 and 5 combined and shorter than segment 3, segment 4 much longer than segment 5. Facial length and width as 7.3:6.3; postocellar line subequal to ocellocular line; ocelloccipital line two-thirds as long as postocellar; clypeus moderately convex, apex slightly wavy; punctures finer than those on rest of face, with apical impunctate band narrow, being one-fourth as wide medially as greatest width of scape; eye with relative length and width as 6.5:2.8, as wide as genal area; inner margins of eyes converging below; hypostomal carina rather low, decreasing gradually from angle toward rear; scape subequal to combined lengths of antennal segments 2 to 4; pedicel half as long as segment 2; flagellum with segment 1 more than half as long as segment 2, last segment slightly longer than a typical segment, unmodified. Middle leg with tibial spine almost as long as to little longer than that of foreleg; strigilis with apex of velum truncate, inner apical angle almost semicircular; malus with apex produced into a short, slender, slightly downward and outward projecting spine; velum wider at apex than at base. *Mesosoma:* Foreleg with segments of mediotarsus slightly swollen, tarsal segment 2 slightly longer than wide at apical end, segments

3 and 4 progressively shorter and narrower (anterior lobes more produced than posterior lobes); basitarsus gradually thickened from base to apex where it is about one-fourth as broad as long. Middle leg with coxa unmodified, tarsal segments 2 and 3 swollen, with anteroposterior width more than width of basitarsus; hind basitarsus almost uniformly broad from base to apex, fully five times as long as broad; hind tibial spurs long, slender, inner one longer and less curved apically than outer. Forewing with maximum length and width as 7:2.3, papillae on apex fine and dense, hairs on cells long and sparse. Propodeal triangle shining and wrinkled above and aciculate below. *Metasoma:* Terga 2 to 6 with apical impunctate bands fully one-seventh as wide as punctate portions and shining; sixth tergum slightly reflexed laterally and apically, midapex with a shallow emargination (absent in some); produced portion of tergum 7 with wide and shallow midapical emargination, on each side of which the projection is short and bluntly right angular. Metasomal sternum 1 with very shallow midapical emargination; sternum 2 broadly rounded, often straight or feebly emarginate medially, with apical fringe of long black hairs; sternum 3 with midapical emargination deep, nearly one-third as wide as sternum, fringed with long light brown hairs; sternum 4 with median third produced, apex broadly truncate and covered with coarse black hairs; sternum 6 with broad midapical projection, covered with short curved bristles, apex convexly arcuate and wider than base; sternum 8 truncate apically except for long, slender median process which is uniformly wide throughout length, and a little less than one-third total length of sternum. Gonocoxite with a few long hairs mesally, basal to angle, and with tuft of anterolaterally directed medium-sized hairs on ventrolateral surface of angle, apical process slightly pointed, directed mesad; penis-valves slightly arcuate; volsella subtriangular at free posterior end.

Female: Length of body 9 mm. *Coloration:* Dark blue, dorsum of head and thorax greenish; mandibles, antenna, legs, and center of abdomen black. *Pubescence:* Hair on upper half of face, vertex, dorsum of thorax, propodeum, and metasomal tergum 2 black and white mixed (white predominant on supra-antennal area and on thorax); metasomal tergum 1, except a few lateral black hairs, white; pubescence otherwise black; anterior margin of foretarsus with black hooked hairs, posterior surface with erect, longer, curved hairs which are increasingly L-shaped towards the apex; hairs on hypostomal area curved at apices, directed anteromesally. *Head:*

Mandible with superior apical angle (tooth 1) slightly acute, tooth 2 present, rather small, midway between 1 and 3; teeth 1, 3, and 4 almost equidistant; teeth 3 and 4 triangular, 4 twice as long as 3, slender, separated from tooth 3 by wide notch; mandibular carinae strongly raised, narrow, lower two equal and parallel, upper sinuous, curving down apically and reaching base of tooth 3; mandible with apex slightly less than 1.5 times as wide as constriction, which is scarcely narrower than base; labial palpus with segment 1 almost equal to segment 2. Facial length and width as 7.2:5.8; postocellar line slightly less than ocellocular line; ocelloccipital line nearly 1.5 times as long as postocellar line; clypeus convex, punctures subapically equal to those on rest of face, coarser centrally and basally, apical impunctate band almost as wide laterally as greatest width of scape, apical margin thickened and swollen laterally, showing a median depression when viewed from above; eye about three times as long as wide, base of mandible about as wide as eye; inner margins of eyes slightly converging below; flagellar segment 1 twice as long as pedicel; hypostomal carina moderately high, highest well behind angle, gradually reduced from point of greatest height; hypostomal area convex, punctures coarse. *Mesosoma:* Foreleg with tibial spine slightly shorter than that on middle leg; forebasitarsus with longest hair little more than half as long as basitarsus; strigilis with apex obliquely truncate, spine short, directed straight forward, inner apical angle of velum sharp, inner basal angle rounded; hind tibial spurs long, slender, curved only at tips. Forewing with maximum length and breadth as 7.2:2.5; papillae on apex fine, dense, hairs on cells short and dense. *Metasoma:* Terga 1 to 5 with apical impunctate bands broad, finely lined and shining, band on tergum 2 one-third as wide as exposed part.

Type material: Holotypes of *pikei*, from Halfway House, Pike's Peak, Colorado, of *universitatis* from Boulder, Colorado, of *amala* from Florissant, Colorado, and of *metitia* from Boulder, Colorado, are in the United States National Museum. The type of *integrella* from Boulder, Colorado, has not been located. Sandhouse (1939) states that it is in "Cockerell's collection" but Dr. Hugo G. Rodeck of the University of Colorado Museum has informed me that it is not in the collection of that institution.

Distribution: British Columbia to California, east to Wyoming and Colorado. Besides the type material, specimens have been studied by us from the following localities:

BRITISH COLUMBIA: Vernon, August 5, 1907. WASHINGTON: Olympia; Seattle. OREGON: high Cascade Mountains, Linn County, July 20, 1909 (J. C. Bridwell); Corvallis, April 26, 1926 (H. A. Scullen), April 17, 1947 (L. E. Wallace). CALIFORNIA: Los Angeles (W. H. Ashmead collection; this record is presumably an error but may indicate the existence of the species in the mountains of Los Angeles County). COLORADO: Boulder, May 22, 1913; spring, 1931 (P. Lundy); April 15, 1933 (H. W. Campbell); Geneva Park, May 14, 1929 (H. Rodeck); Jefferson, June 27, 1913 (A. K. Fisher).

Osmia (*Centrosmia*) *austromaritima* Michener

Osmia austromaritima Michener, 1936, Canadian Ent., vol. 68, p. 43; Bohart, Knowlton, and Bailey, 1950, Utah State Agr. College, Mimeographed ser. no. 371 (male).

Osmia (*Nothosmia*) *austromaritima*, Sandhouse, 1939, Mem. Ent. Soc. Washington, no. 1, p. 85.

This species closely resembles *pikei, thysanisca, raritatis,* etc. but differs in having more black hairs on the genal and pleural areas, deeper emarginations of the seventh metasomal tergum and the third metasomal sternum, in lacking a median patch of coarse black hairs on the fourth metasomal sternum, in the equal width of the genal area and eye, in the greater length of the tibia in proportion to the width, and in the much longer and coarser hairs at the apical angle of the gonocoxite.

Male: Length of body 8 to 10 mm. *Coloration:* Mandible dark brown to black; flagellum dark above, light below, legs dark brown with weakly metallic femora; face, vertex and dorsum of head dark bluish green; genal area, side of thorax, propodeum, metasomal terga deep blue. *Pubescence:* Hairs on face, vertex, dorsum of thorax, and metasomal tergum 1 (except on side) white, on second tergum, thoracic sternum, and genal area white mixed with black; on hypostomal area dusky; on metasomal sterna (except golden, midapical fringe on third) fuscous; on lower surfaces of tarsal segments reddish brown; on rest of body black. *Head:* Mandible with a wide, deep, V-shaped notch separating upper tooth from very long, lower tooth; apical edge above notch straight or slightly rounded, superior apical angle slightly obtuse; apical edge above notch at right angles to base of lower tooth; mandibular carinae parallel, lower carina apically at least three times as wide as upper, narrower basally, space between them narrow; labial palpus with relative lengths of segments 1 and 2 as 11:13; maxillary palpus

with segment 3 longer than segment 2, subequal to combined lengths of segment 4 and 5; segment 5 much shorter and narrower than segment 4; face slightly longer than wide; postocellar line nearly equal to ocellocular line; ocelloccipital line a little more than two-thirds as long as postocellar; clypeus convex, apex with median one-third produced, a shallow median emargination at apical margin of projection, punctures finer than those surrounding area, apical impunctate band about half as wide medially as greatest width of scape; scape subequal to antennal segments 2 to 4 combined; pedicel half as long as flagellar segment 1; flagellum with last segment slightly longer than any typical segment, unmodified; eye with relative length and width as 5.2:2.7, nearly as wide as genal area; inner margins of eyes converging below; hypostomal carina moderately low, highest far behind angle. *Mesosoma:* Middle leg having tibial spine longer than that of foreleg; strigilis with apex of velum truncate; malus with apex produced into a long sharp spine, which projects slightly downwards, spine one-fifth as long as entire length (including spine); malus with width at base twice the width of velum at base; velum with inner basal angle more narrowly rounded than inner apical angle; foreleg with segments of mediotarsus slightly swollen, segment 2 as wide as long, segments 3 and 4 progressively shorter, narrower, basitarsus over three times as long as wide; middle leg with coxa unmodified, tarsal segments 2 and 3 swollen, scarcely wider than basitarsus, swelling equally produced on each side; tarsal segment 2 slightly longer than wide, segment 3 as long as wide; hind basitarsus widest medially, truncate apically; hind tibial spurs long and slender, apices slightly curved. Forewing with relative maximum length and width as 5.8:2, papillae on apex fine, sparse; hair on cells long and sparse. Propodeal triangle wrinkled above, aciculate below. *Metasoma:* Terga 2 to 5 with apical impunctate bands about one-third or one-fourth as wide as punctate portions, shining; tergum 6 with equally wide apical impunctate portion slightly turned up, midapex without emargination; tergum 7 with deep, wide emargination at midapex of produced portion, depth nearly equal to width of emargination, teeth on each side slender, pointed. Sternum 1 having shallow, wide midapical emargination, long posteriorly directed black hairs on entire sternum; sternum 2 with broadly rounded apical margin, hairs similar to those of first, restricted to subapical lateral areas; sternum 3 with midapical concavity deep, wide (nearly one-third width of sternum) fringed with

long golden hairs, black hairs shorter than those on first and second; sternum 4 with median third produced medially and apically, almost truncate, median apical patch of golden hairs bent mesad at tips; sternum 5 with apical margin deeply emarginate; basal margin of sternum 6 strongly concave, posteromedian portion with short hamate bristles in a patch which is V-shaped anteriorly, apical margin with middle third rounded and produced, with a V-shaped median emargination; sternum 8 similar to that of *thysanisca*. Gonocoxite broad and of uniform width throughout length, with tufts of long, coarse hairs on inner and outer sides of subapical angulation; penis valve forcepiform; volsella subtriangular; apical process of gonocoxite stout.

Type material: Holotype male, obtained by C. D. Michener at San Pedro Hills, Los Angeles County, California, February 22, 1929, is in the Snow Entomological Museum, University of Kansas.

Distribution: California to Utah and Colorado. In addition to the type, the following specimens have been studied.

CALIFORNIA: Viola, May 15, 1909. UTAH: Green Canyon, Cache County, April 15, 1943 (G. F. Knowlton, D. R. Maddock, S. L. Wood). The species was recorded by Sandhouse (1939) from Colorado, but she gave no locality data. Therefore, it has not been possible to evaluate or verify the record or get any idea of the part of Colorado in which this species occurs.

Osmia (*Centrosmia*) *vandykei* Sandhouse

Osmia vandykei Sandhouse, 1924, Proc. California Acad. Sci., ser. 4 vol. 13, p. 344; Sandhouse, 1939 Mem. Ent. Soc. Washington, no. 1 p. 86 (male).

This species does not closely resemble any other member of the subgenus *Centrosmia,* although it resembles *pikei* in the shape of the genitalia, the swollen midtarsal segments of the middle legs, the shallow emargination of the apical margin of the sixth metasomal tergum, the deep and confluent punctation of the face, vertex and genal area, the elongated malar spine of the strigilis, and the general shape of sixth metasomal sternum. But a large number of characters, including the shape of the apex of the clypeus, the flattened expanded apical segment of the flagellum, the concavities on the under side of the swollen midtarsal segments of the middle leg, the long stiff hairs on the expanded sides of the fifth, sixth and seventh metasomal terga, and shape of the posteromedian portions of the sixth and seventh metasomal terga, distinguish this species from all others.

Male: Length of body, 10 mm. *Coloration:* Dark blue, sometimes greenish; flagellum dark above, light brown below; legs dark brown; face, vertex and dorsum of thorax greenish blue. *Pubescence:* Hair on face, vertex, dorsum of thorax, mesepisternum, hypostomal area, underside of femur and tibia of foreleg, part of lateral area of first metasomal tergum, and apical bands of hairs on second and third metasomal terga white; on remaining parts dusky to black, except reddish brown on undersides of fore and middle tarsi. *Head:* Mandible with narrow, deep, V-shaped notch separating sharply acute upper tooth from long slender sharp lower tooth, upper apical edge above notch slanting, lower broadly concave (widths of upper and lower teeth equal at bases); mandibular carinae convergent towards base of lower tooth; upper carina about one-third as wide as lower carina on apical portion, equal near base, space between them narrow; facial length and width as 6.6:6; postocellar line subequal to ocellocular line; ocelloccipital line nearly two-thirds as long as postocellar; clypeus convex, midapex produced into a very small rounded projection anteriorly, punctures finer than those on rest of face, apical impunctate band about three-fourths as wide medially as greatest width of scape; scape nearly as long as combined length of antennal segments 2 to 4; pedicel half as long as flagellar segment 1; flagellum with segments 9 to 10 progessively wider, segment 11 most strongly compressed and widest, outer edge convex, apex rounded; eye more than twice as long as wide; relative widths of eye and genal area as 3:2.2; inner margins of eyes weakly converging below; hypostomal area of uniform height throughout; labial palpus with relative lengths of segments 1 and 2 as 8:10; maxillary palpus with relative lengths of segments 2 to 5 as 5:7:5:3. *Mesosoma:* Middle leg with tibial spine slightly longer than that on foreleg; strigilis with apex of velum truncate, inner apical angle more broadly rounded than inner basal angle; malus with apex abruptly produced into a thin, sharp spine projecting sharply downward; malus about twelve times as long as spine; velum at base one-third as wide as malus at base; foreleg with segments of mediotarsus slightly swollen, subequal in width, longer than wide, progressively shorter from tarsal segment 2 to 4; basitarsus uniformly widened apically, two and one-half times longer than wide; middle leg with coxa unmodified, tarsal segments 2 and 3 greatly swollen posteriorly (inner surfaces deeply concave), as wide as long; tarsal segment 4 not swollen; hind basitarsus almost parallel sided, truncate at apex; hind tibial spurs slender, distinctly curved apically. Forewing three

times as long as wide, papillae on apex fine and sparse; hair on apical cells short and moderately dense, on basal cells longer and more sparse. *Metasoma:* Terga 1 to 5 with apical impunctate bands, each band nearly one-fifth as wide as punctate portion and shining; tergum 6 with median portion and 7 with median-basal and lateral portions covered by very long and erect hairs; tergum 6 with apical margin broadly very shallowly emarginate; tergum 7 with apex greatly thickened laterally, weakly emarginate medially, resultant lobes very obtuse. Sternum 1 with a moderately deep, narrow midapical emargination; sternum 2 with hair long on apical portion, apical margin convex; sternum 3 with a deep, wide V-shaped emargination, margin of V lined with a row of golden hairs progressively longer towards apex, long posteriorly directed, black hair on each side of emargination; sternum 4 impunctate and without hairs except for a broad subtriangular patch of slightly curled blackish bristles which is divided basally by a longitudinal impunctate stripe, apical margin with a median, truncate, produced portion which has a fimbria of plumose hair; sternum 6 with a deep basal emargination, posteromedian portion with a broadly subtriangular patch of coarse hamate bristles, apical margin with middle third truncate and strongly produced; sternum 8 subtriangular, with a long, slender, apical process which is as long as triangular portion. Gonocoxite with well-marked constriction and a single long bristle on dorsal surface nearly opposite apex of volsella, beyond and lateral to apical process a group of stiff hairs which are directed latero-posteriorly, mesal surface with several long hairs basad of process; volsella with apex broadly subtriangular; penis valve curved near apex.

Type material: Holotype male and one paratype male, collected by E. C. Van Dyke at Fremont National Forest, Klamath County, Oregon, on June 18, 1922, are in the California Academy of Sciences, San Francisco, California.

Distribution: Washington to southern Oregon. The following specimens have been examined by us: WASHINGTON: Pullman. OREGON: Wildhorse Canyon, Andrews, 4270 feet altitude, July 5, 1927 (H. A. Scullen).

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The Comparative Morphology, Phylogeny and Higher Classification of the Butterflies (Lepidoptera: Papilionoidea)[1]

BY

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ABSTRACT: This paper is the second and final section of a work on the integumental morphology, phylogeny and classification of the butterflies. It is based primarily on a detailed comparative morphological study of some 250 genera of butterflies and a less comprehensive study of representatives of 24 families of moths. The relationship of the butterflies to the remainder of the Lepidoptera is discussed as are the interrelationships of the various families and subfamilies of the butterflies themselves. A relatively conservative higher classification of the butterflies is proposed in which they are divided into the following families and subfamilies: Papilionidae (Papilioninae, Parnassiinae, Baroniinae); Pieridae (Pierinae, Coliadinae, Dismorphiinae, Pseudopontiinae); Nymphalidae (Ithomiinae, Danainae, Satyrinae, Morphinae, Charaxinae, Calinaginae, Nymphalinae, Acraeinae); Libytheidae; Lycaenidae (Lycaeninae, Styginae, Riodininae).

INTRODUCTION

This is the second section of a work on the comparative morphology, phylogeny and higher classification of the butterflies. The first section (Ehrlich, 1958) dealing with the detailed integumental anatomy of the adult monarch butterfly (*Danaus plexippus* L.) laid the necessary foundation for the comparative morphological studies which are the central theme of the present work. An attempt has been made to integrate the new morphological data resulting from this study with pre-existing data (principally morphological) in order to provide the broadest possible base for the conclusions drawn.*

SYSTEMATIC PRINCIPLES

Complete objectivity in arriving at classifications and phyletic relationships is at present a utopian concept, although advances are being made in this direction (see Michener and Sokal, 1957).

Some major sources of subjective error in taxonomic work are: 1) preconception (to some degree unavoidable when a worker is dealing with a group with which he has long been familiar); 2) unjustified character weighting (especially a tendency to give more weight to characters studied personally); 3) group favoritism (the tendency to consider one's favorite taxonomic group as higher in the hierarchy of classification than equivalent groups); and 4) frankly subjective decisions ("I feel that the Xidae are worthy of family rank" or "*Yus* is obviously more closely related to *Zus* than *Xus*"). Every attempt has been made to avoid these errors in the present work, but doubtless numbers 1 and 2 have not been completely eliminated. It is hoped that 3 and 4, abundantly represented in the literature, have been entirely excluded.

There are those (*e. g.*, Warren, 1947) that claim that higher categories should be based on the distribution of one or two diagnostic characters. This is an unfortunate concept which may easily lead to polyphyletic taxa and erroneous ideas of relationship. It should be pointed out that a character state found in all known members

* Characters of the larvae have been considered only rarely in this work. Unfortunately, there is a general lack of systematic information on these forms, especially of the homologies of their structures (*e. g.*, tubercles on one larva are not necessarily homologous to tubercles on another). It should be noted that characters of the larvae are neither more nor less significant than those of the adult, and that properly conducted investigations of *large numbers* of larval characters would provide an interesting independent check of the conclusions arrived at here primarily on the characters of the imagines.

of a group (a diagnostic character) is probably of no greater significance from the viewpoint of phylogeny than one found in, say, 97 percent of the known members of a group. Whether the absence of a well developed third vannal vein (3 V) in the hindwings was a diagnostic character of the Papilionidae hinged on the discovery of *Baronia brevicornis,* a rare papilionid unique in its family in possessing the vein. Many similar cases could be cited. The repeated failure of systems based on too few characters to stand the test of time is a matter of record and will not be discussed further here. In the present work the number of characters considered has been limited by time and practicality, but it is hoped that the sample has been sufficiently large to avoid major errors.

The question of the nomenclatorial status of the various taxa segregated has received considerable attention. Some previous classifications of butterflies, as exemplified by Clark (1948) have presented entomologists with a mass of largely undefined families, subfamilies, tribes and subtribes within the superfamily Papilionoidea. Fortunately, this extreme splitting has been largely ignored.

In the present work it has been found that the Papilionoidea divide primarily into five groups. In an attempt to align the classification of butterflies with that of other superfamilies of insects these five groups have been called families (Papilionidae, Pieridae, Nymphalidae, Libytheidae, Lycaenidae). The Apoidea (6 families) show much greater morphological and behavioral diversity than the butterflies. The Sphecoidea (3 to 18 families) show a variety of form and habits not even faintly approached in the Papilionoidea, as do the Fulgoroidea (which some authorities consider to represent a single family, the Fulgoridae). The same is true of the Chalcidoidea, Scaraboidea, Tipuloidea and others. Within these groups the major divisions are considered to be families. While it is difficult to compare and equate differences within major groups, it seems evident that the recognition of the primary divisions of the Papilionoidea with superfamilial designations such as "family group" would not be in keeping with accepted entomological practice.

As far as possible the morphological distinctness of the various taxa has been kept uniform within the next highest taxon. Thus, in order to have all the families in the superfamily more or less equivalent, the long standing "families" into which the nymphalids have been split previously must be considered to be subfamilies, since their elevation to family rank would necessitate the raising

to family rank of all the tribes of the Papilionidae, a move which has not been advocated even by the most extreme "splitters." The degree of morphological distinctness of subgroups may vary greatly among higher taxa. By "morphological distinctness" is meant both the actual degree of morphological difference (*e. g.*, presence or absence of a structure is ordinarily considered a greater difference than change of size or shape in a structure) and also the size of the gap between character states (*i. e.*, whether the variation is essentially continuous or, if not, the degree of discontinuity). Thus the subfamilies of the Nymphalidae have smaller gaps separating them and show less morphological diversity than those of the Papilionidae. This difficulty is inherent in the nomenclatorial system as usually interpreted. The only alternative that might help to give subfamilies in these two families equivalent rank would be to place all nymphalids in a single subfamily, more or less comparable to the papilionid subfamilies. This subfamily could then be divided into tribes. In view of the size of the Nymphalidae, this heterodox system seems undesirable.

Much of the difficulty in butterfly (and other) nomenclature can be traced to workers who, starting at the specific level, have deemed it necessary to recognize nearly every branching of the phylogenetic tree with a supraspecific taxon. Using this system one is not far down the tree when the family level is reached, and the result is a large mass of family names with meaning only to specialists. For the benefit of other biologists it is suggested that conservatism (*i. e.*, "lumping") be the rule at the ordinal, familial and generic levels. The complexities of phylogeny can be shown equally well with the aid of less important categories such as sub- and superfamily, tribe, subgenus, species group, etc.

The concept of the family Nymphalidae is a meaningful one to almost every entomologist and to many other biologists. It can be used without misgivings in ecological or experimental work, and is easily explained to beginning students. It is doubtful if the family Apaturidae is a meaningful entity to one in a thousand entomologists. Since convenience is the only excuse for nomenclature the conclusions seem obvious.

MATERIAL AND METHODS

Some 240 genera and 300 species of butterflies were dissected in the course of the present work as well as 41 representatives of 24 families of moths and skippers. Dried specimens were used ex-

clusively. The wings were removed and preserved, along with locality labels (if any), in glassine envelopes. The body was then wetted with 80 percent alcohol and heated in 10 percent KOH until the viscera were soft (semiliquid). The specimens were then dissected under water, the scales being removed with brushes and the viscera with watchmakers forceps and pipettes. The dissected specimens were preserved in 80 percent alcohol.

Only determined specimens were used. It did not prove practical to verify all specific identifications, but all doubtful generic determinations were checked. The generic nomenclature employed has been made as up to date as possible; however, wherever a group has been commonly considered either a subgenus or a genus (*e. g., Graphium, Zerene*) it has been retained as a genus in order to accent the variety of the sampling. Since this paper is not primarily nomenclatorial, in no case does the use of such a name indicate endorsement of the usage employed.

The genera and species examined are listed below by families, and placed alphabetically within the families. Except for the entities marked with an asterisk all were dissected as described above. Those marked with the asterisk were examined for superficial characters. Every character has not been examined in every species, since ordinarily only one sex of each species was dissected, and since sometimes parts were missing or damaged. It is hoped that this deficiency has been compensated at least in part by the large number of genera and species examined.

Non-papilionoids Studied

HEPIALIDAE: *Hepialus humuli* Linnaeus; MEGALOPYGIDAE: *Megalopyge opercularis* Smith; ZYGAENIDAE: *Zygaena minos* Fuessly; EUCLEIDAE: *Sibine stimulea* Clemens; TINEIDAE: *Tinea pellionella* Linnaeus; GELECHIIDAE: *Gelechia serotinella* Busck; YPONOMEUTIDAE: *Atteva aurea* Fitch: AEGERIIDAE: *Melittia satyriniformis* Hübner; OLETHREUTIDAE: *Carpocapsa pomonella* Linnaeus, *Exartema fasciatanum* Clemens; COSSIDAE: *Prionoxystus robiniae* Peck; CASTNIIDAE: *Castnia atymnius* Dalman, *Castnia licus* Fabricius; THYRIDIDAE: *Thyris lugubris* Boisduval; PYRALIDAE: *Crambus vulgivagellus* Clemens, *Desmia funeralis* Hübner, *Galleria mel'onella* Linnaeus, *Loxostege similalis* Guenée, *Nymphula icciusalis* Walker; PTEROPHORIDAE: *Oidaematophorus monodactylus* Linnaeus; URANIIDAE: *Chrysiridia leilus* Linnaeus, *Chrysiridia madagascariensis* Lesson; SATURNIIDAE: *Actias luna* Linnaeus, *Eacles imperialis*

Drury; LASIOCAMPIDAE: *Tolype distincta* French; GEOMETRIDAE: *Haematopis grataria* Fabricius; SPHINGIDAE: *Celerio lineata* Fabricius; NOTODONTIDAE: *Datana ministra* Drury; PHALAENIDAE: (= NOCTUIDAE): *Agrotis ypsilon* Rottemburg, *Catocala cerogama* Guenée, *Peridroma margaritosa* Hübner, *Polia adjuncta* Boisduval; AMATIDAE: *Ctenucha* sp.; ARCTIIDAE: *Haploe* sp., *Utethesia bella* Linnaeus; HESPERIIDAE: *Adopaea lineola* Ochsenheimer, *Calpodes ethlius* Cramer, *Erynnis juvenalis* Fabricius, *Megathymus neumoegeni* Edwards, *Poanes zabulon* Boisduval and Leconte, *Proteides clarus* Cramer.

Papilionidae Studied

Archon apollinus Herbst, *Baronia brevicornis* Salvin, *Battus polydamus* Linnaeus, *Battus philenor* Linnaeus, *Battus devilliers* Godart*, *Bhutanitis lidderdalei* Atkinson, *Cressida cressida* Fabricius, *Euryades duponcheli* Lucas, *Graphium agamemnon* Linnaeus*, *Graphium agesilaus* Guérin and Percheron*, *Graphium agates* Westwood*, *Graphium antiphates* Cramer, *Graphium bathycles* Zinken*, *Graphium celadon* Lucas*, *Graphium cloanthus* Westwood, *Graphium columbus* Kollar*, *Graphium dolicaon* Cramer*, *Graphium epidaus* Doubleday*, *Graphium eurypylus* Linnaeus*, *Graphium evemon* Boisduval*, *Graphium harmodius* Doubleday*, *Graphium leonidas* Fabricius, *Graphium macareus* Godart, *Graphium marcellus* Cramer, *Graphium nomius* Esper*, *Graphium pausanias* Hewitson, *Graphium payeni* Boisduval*, *Graphium philolaus* Boisduval* *Graphium policenes* Cramer*, *Graphium protesilaus* Linnaeus*, *Graphium sarpedon* Linnaeus, *Graphium thymbraeus* Boisduval, *Graphium xenocles* Cramer*, *Hypermnestra helios* Nickerel, *Lamproptera* (= *Leptocircus*) *curius* Fabricius, *Lamproptera meges* Zinken*, *Leuhdorfia puziloi* Erschov, *Ornithoptera priamus* Linnaeus, *Papilio aegius* Donovan*, *Papilio alexiares* Hopffer*, *Papilio anchisiades* Esper*, *Papilio aristius* Cramer*, *Papilio aristodemus* Esper*, *Papilio bianor* Cramer*, *Papilio castor* Westwood*, *Papilio chaon* Westwood*, *Papilio cresphontes* Cramer, *Papilio cynorta* Fabricius, *Papilio demetrius* Cramer, *Papilio demolion* Cramer*, *Papilio eurymedon* Lucas*, *Papilio glaucus* Linnaeus, *Papilio hectorides* Esper, *Papilio indra* Reakirt*, *Papilio machaon* Linnaeus, *Papilio memnon* Linnaeus*, *Papilio montrouzieri* Boisduval*, *Papilio multicaudatus* Kirby*, *Papilio paeon* Boisduva*, *Papilio palamedes* Drury*, *Papilio paris* Linnaeus*, *Papilio pilumnus* Boisduval*, *Papilio polyxenes* Fabricius, *Papilio proneus* Hübner*, *Papilio rutulus* Lucas*, *Papilio thoas* Linnaeus*, *Papilio torquatus* Cramer*,

Papilio troilus Linnaeus, *Papilio xuthus* Linnaeus*, *Parides* (= *Atrophaneura*) *arcus* Cramer*, *Parides aristolochiae* Fabricius, *Parides coon* Fabricius*, *Parides latreilli* Donovan*, *Parides montezuma* Westwood*, *Parides mylotes* Bates, *Parides perrhebus* Boisduval*, *Parides philoxenus* Gray, *Parides polydorus* Linnaeus*, *Parides polyzelus* Felder, *Parides rhodifer* Butler*, *Parides sesostris* Cramer, *Parides varuna* White*, *Parnassius apollo* Linnaeus*, *Parnassius clodius* Ménétriés, *Parnassius eversmanni* Ménétriés*, *Parnassius mnemosyne* Linnaeus*, *Parnassius smintheus* Doubleday and Hewitson, *Sericinus telamon* Donovan, *Teinopalpus imperialis* Hope, *Trogonoptera brookiana* Wallace*, *Troides helena* Linnaeus, *Troides rhadamantus* Lucas*, *Zerynthia hypermnestra* Scopoli, *Zerynthia rumina* Linnaeus.

Pieridae Studied

Anteos chlorinde Godart, *Anthocharis midea* Hübner, *Aporia crataegi* Linnaeus, *Appias nephele* Hewitson, *Archonias tereas* Hübner, *Belenois mesentina* Cramer, *Cepora nadina* Lucas, *Colias philodice* Godart, *Colotis achine* Cramer, *Colotis danaë* Doubleday and Hewitson, *Delias eucharis* Drury, *Dismorphia nemesis* Latreille, *Dixeia cebron* Ward, *Euchloe belia* Cramer, *Eurema nicippe* Cramer, *Gonepteryx rhamni* Linnaeus, *Hebomoia glaucippe* Linnaeus, *Itaballia demophile* Linnaeus, *Ixias pyrene* Linnaeus, *Kricogonia lyside* Godart, *Leptidea sinapis* Linnaeus, *Leptophobia aripa* Boisduval, *Leptosia xiphia* Fabricius, *Leucidea brephos* Hübner, *Melete isandra* Boisduval, *Nathalis iole* Boisduval, *Neophasia menapia* Felder, *Pereute callinira* Staudinger, *Perrhybris pyrrha* Cramer, *Phoebis sennae* Linnaeus, *Pieris protodice* Boisduval and Leconte, *Prioneris thestylis* Doubleday, *Pseudopieris nehemia* Boisduval, *Pseudopontia paradoxa* Felder, *Zerene eurydice* Boisduval, *Zegris fausti* Christopher.

Nymphalidae Studied

Acraea encedon Linnaeus, *Acraea esebria* Hewitson, *Acraea natalica* Boisduval, *Acraea* sp., *Actinote carycina* Jordan, *Actinote neleus* Latreille, *Actinote ozomene* Godart, *Ageronia amphinome* Linnaeus, *Agraulis vanillae* Linnaeus, *Amathusia phidippus* Johannson, *Amauris ochlea* Boisduval, *Amauris psyttalea* Plötz, *Anadebis himachala* Moore, *Anaea andria* Scudder, *Anaea appias* Hübner, *Antirrhaea miltiades* Fabricius, *Apatura iris* Linnaeus, *Aprotopus aedesia* Doubleday and Hewitson, *Araschnia levana* Linnaeus, *Asterocampa celtis* Boisduval and Leconte, *Bia actorion* Linnaeus,

Boloria toddi Holland, *Brassolis astyra* Godart, *Brassolis sophorae* Linnaeus, *Byblia ilythea* Drury, *Caligo* sp., *Calinaga buddha* Moore, *Callerebia annada* Moore, *Callicore marchalii* Guérin, *Callitaera aurora* Felder, *Callithomia hezia* Hewitson, *Catagramma maimuna* Hewitson, *Catonephele numilia* Cramer, *Catuna crithea* Drury, *Ceratinia titutia* Hewitson, *Ceratinia vallonia* Hewitson, *Cethosia chrysippe* Felder, *Charaxes brutus* Cramer, *Charaxes psaphon* Westwood, *Chlosyne janais* Drury, *Cirrochroa malaya* Felder, *Clothilda numida* Hübner, *Coenonympha hero* Linnaeus, *Coenophlebia archidona* Hewitson, *Corades inyo* Hewitson, *Cupha grymanthis* Drury, *Cynthia arsinoë* Cramer, *Cyrestis nivalis* Felder, *Danaus cleona* Stoll, *Danaus plexippus* Linnaeus, *Dichorragia nesimachus* Boisduval, *Didonis biblis* Felder, *Dione juno* Cramer, *Dircenna klugii* Hübner, *Discophora sondaica* Boisduval, *Doleschallia bisaltide* Cramer, *Doxocopa cyane* Latreille, *Doxocopa laurentia* Godart, *Dryadula phaetusa* Linnaeus, *Dryas iulia* Hübner, *Dynastor darius* Felder, *Elymnias hypermnestra* Linnaeus, *Elymnias malelas* Hewitson, *Elymniopsis bammakoo* Westwood, *Enispe euthymius* Doubleday, *Epinephile jurtina* Linnaeus, *Erebia epipsodea* Butler, *Ergolis ariadne* Linnaeus, *Eryphanis aesacus* Herrich-Schäffer, *Eueides aliphera* Godart, *Eueides thales* Cramer, *Euphoedra eleus* Drury, *Euphoedra medon* Linnaeus, *Euphydryas chalcedona* Doubleday and Hewitson, *Euphydryas phaeton* Drury, *Euploea core* Cramer, *Euploea diocletianus* Fabricius, *Euptoieta claudia* Cramer, *Euptychia hesione* Sulzer, *Euthalia garuda* Moore, *Faunis assamus* Westwood, *Faunis canens* Hübner, *Gynaecia dirce* Linnaeus, *Gyrocheilus patrobas* Hewitson, *Haematera thysbe* Doubleday and Hewitson, *Haetera piera* Linnaeus, *Heliconius charithonia* Linnaeus, *Heliconius chestertoni* Hewitson, *Heliconius hortense* Guérin, *Heterochroa bredowii* Geyer, *Hirsutis neitha* Hopffer, *Historis odius* Fabricius, *Hypna clytemnestra* Cramer, *Hypoleria andromica* Hewitson, *Hypolimnus bolina* Linnaeus, *Hypolimnus dubia* Aurivillius, *Idea idea* Linnaeus, *Ideopsis gaura* Horsfield, *Ithomia cleora* Hewitson, *Ituna phenareta* Doubleday, *Kallima inachus* Boisduval, *Lethe eurydice* Johannson, *Lethe kansa* Moore, *Lethe sura* Hewitson, *Limenitis bredowii* Geyer, *Limenitis populi* Linnaeus, *Lycorea cleobaea* Godart, *Marpesia petreus* Bates, *Mechanitis doryssus* Bates, *Megistanis baeotus* Doubleday and Hewitson, *Melanargia galathea* Linnaeus, *Melanitis leda* Drury, *Melinaea paraiya* Reakirt, *Melitaea artemis* Schiffermuller, *Melitaea dymas* Edwards, *Metamorpha steneles* Linnaeus, *Minois pegala* Fabricius, *Morpheis ehrenbergi*

Hübner, *Morpho achilles* Linnaeus, *Morpho aratos* Fruhstorfer, *Morpho hecuba* Linnaeus, *Morpho laertes* Druce, *Morpho sulkowskyi* Kollar, *Napeogenes thira* Hewitson, *Narope cyllabarus* Westwood, *Neope goschkevitschii* Ménétriés, *Neptis vikasi* Horsfield, *Nessaea obrinus* Linnaeus, *Nymphalis polychloros* Linnaeus, *Oeneis semidea* Say, *Opoptera sulcius* Staudinger, *Opsiphanes invirae* Hübner, *Panacea prola* Doubleday and Hewitson, *Pandita sinoria* Felder, *Pantoporia opalina* Kollar, *Pararge megera* Linnaeus, *Pardopsis punctatissima* Boisduval, *Parthenos gambrisius* Fabricius, *Perisama bonplandii* Guérin, *Philaethria dido* Clerck, *Phyciodes tharos* Drury, *Pierella lamia* Sulzer, *Planema aganice* Hewitson, *Precis* sp., *Prepona chromus* Guérin, *Pronophila thelebe* Doubleday and Hewitson, *Pseudergolis wedah* Kollar, *Pyrrhogyra typhoeus* Felder, *Ragadia crisilda* Hewitson, *Sais rosacia* Cramer, *Salamis cytora* Doubleday and Hewitson, *Satyrus circe* Fabricius, *Satyrus semele* Linnaeus, *Scada theaphia* Bates, *Smyrna blomfieldia* Fabricius, *Speyeria cybele* Fabricius, *Stibochiona nicea* Gray, *Stichophthalma camadeva* Westwood, *Taenaris phorcas* Westwood, *Taygetis ypthima* Hübner, *Tellervo zoilus* Fabricius, *Temenis laothoë* Cramer, *Thyridia confusa* Butler, *Tithorea harmonia* Cramer, *Yoma sabina* Cramer.

Libytheidae Studied

Libythea celtis Fuessly, *Libythea geoffroy* Godart, *Libythea laias* Trimen, *Libythea myrrha* Godart, *Libytheana bachmanni* Kirtland.

Lycaenidae Studied

Abisara neophron Hewitson, *Amblypodia micale* Blanchard, *Anatole zygia* Hübner, *Ancyluris inca* Saunders, *Anteros carusius* Westwood, *Apodemia mormo* Felder, *Apodemia nais* Edwards, *Atlides halesus* Cramer, *Bacotis bacaenis* Hewitson, *Calephelis iris* Staudinger, *Callictita cyora* Bethune-Baker, *Callophrys rubi* Linnaeus, *Candalides dimorphus* Röber, *Candalides meeki* Bethune-Baker, *Caria lampeto* Godman and Salvin, *Cupido minima* Fuessly, *Curetis bulis* Doubleday and Hewitson, *Deudoryx epijarbas* Moore, *Dodona durga* Kollar, *Durbania amakosa* Trimen, *Echenais aristus* Stoll, *Elaphrotis telephus* Cramer, *Euselasia aurantiaca* Godman and Salvin, *Euselasia eulione* Hewitson, *Euselasia mys* Herrich-Schäffer, *Fenesica tarquinius* Fabricius, *Helicopis cupido* Linnaeus, *Hemiargus hanno* Stoll, *Hypochrysops rex* Boisduval, *Hypolycaena philippus* Felder, *Ialmenus evagoras* Hübner, *Incisalia augustinus* Westwood, *Lasaia sessilis* Schaus, *Leucochimona lagora* Herrich-Schäffer,

Lycaena helloides Boisduval, *Lycaenopsis pseudargiolus* Boisduval and Leconte, *Lymnas iarbas* Fabricius, *Lysandra coridon* Poda, *Mampava nigronotata* Bethune-Baker, *Megalopalpus zymia* Doubleday and Hewitson, *Mesosemia telegone* Boisduval, *Metacharis lucius* Fabricius, *Mimacraea dohertyi* Rothschild, *Mitoura gryneus* Hübner, *Nemeobius lucina* Linnaeus, *Niphanda fusca* Bremer and Grey, *Nymphidium cachrus* Fabricius, *Ogyris oroetes* Hewitson, *Philiris innotatas* Miskin, *Plebejus icarioides* Boisduval, *Poretia hewitsoni* Moore, *Pseuderesia libertina* Hewitson, *Rhetus dysonii* Saunders, *Riodina lysippus* Linnaeus, *Satyrium fuliginosa* Edwards, *Siseme alectro* Westwood, *Siseme aristoteles* Latreille, *Stalachtis euterpe* Linnaeus, *Stalachtis phlegia* Cramer, *Stiboges* sp., *Styx infernalis* Staudinger, *Syrmatia dorilas* Cramer, *Taraka hamada* Druce, *Telipna bimacula* Plötz, *Teriomima hildegarda* Kirby, *Tharsalia arota* Boisduval, *Theope mania* Godman and Salvin, *Thestor ballus* Fabricius, *Thisbe irenea* Stoll, *Thysonotas danis* Cramer, *Thysonotis hymetus* Felder, *Zeltus antifaunus* Doubleday and Hewitson, *Zemeros flegyas* Cramer.

To facilitate comparisons all characters in the family diagnoses have been given numbers and all characters in the subfamily diagnoses have been given letters. Thus, in all the families character number one is the shape of the eye, and throughout the subfamilies of the Nymphalidae character "a" is the amount of scaling on the antennae.

All illustrations for the comparative section of this work have been drawn so that the same structures of different genera are the same size. In many cases figure citations refer to illustrations of genera other than those under discussion which show the characteristics alluded to. Citations of figures followed by "-Pt. I" refer to the illustrations of the monarch butterfly in the first section of this work (Ehrlich, 1958).

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COMPARATIVE MORPHOLOGY

This section gives a brief summary, arranged by structures rather than by systematic categories, of the morphological variation found within the butterflies. It emphasizes variation which was found to have taxonomic significance, and variation which was relatively easy to describe. Since many characters which were later found to be of little systematic significance were recorded for about the first 40 genera dissected, these genera appear as a disproportionately high number of the examples cited.

Time has not permitted detailed studies of any organs as have been done by Jordan (1898) on the antennae and Reuter (1897) on the labial palpi. A number of major areas (area of head around and above foramen magnum, axillary sclerites, female genitalia) have been largely ignored because of difficulties in dissecting, describing or comparing them. It is hoped that future studies will fill in these gaps.

The terminology used here is that of the first section of this work (Ehrlich, 1958).

HEAD

With the exception of the majority of the Lycaenidae, the eyes of butterflies are entire. In most lycaenids the eyes are emarginate (*i. e.*, notched opposite the bases of the antennae—see fig. 5), and do not extend caudally as far as those in the other families (figs. 6, 7). Many genera of the Lycaenidae and Nymphalidae have the

eyes hairy to a greater or lesser degree, while they are bare in the remainder of the butterflies.

The structure of the antennae of the butterflies has been the subject of an exhaustive study by Jordan (1898). Of most systematic interest is the variation in the amount of scaling (ranging from completely unscaled to completely scaled) and the arrangement of the antennal sulci and carinae.* A sulcus is a depressed line on the ventral surface of the antenna formed by a groove or series of pits (one to a segment). The carinae are ridges between and flanking the sulci. No original work on the antennal structure has been done in connection with this paper. The carinae are present only in the Nymphalidae and Libytheidae, in which they are almost universal. The presence of the sulci is variable in the Papilionidae and they are usually absent in the Lycaenidae. The antennae of the Pieridae always have one or three sulci.

The distance between the bases of the antennae is very variable, ranging from much less than one half the width of the scape to more than the width of the scape. The area between the antennae may be concave if the antennae are very close together, and there may be a strengthening inflection between the bases of the antennae (the transfrontal suture of DuPorte, 1956). The presence of this inflection is at least to some degree a function of the interantennal distance, it is almost never present when the antennae are close together.

The position of the laterofacial sutures and the concomitant size of the paraocular areas are quite variable. In general the lycaenids have the laterofacial sutures contiguous or nearly contiguous with the eye margins, with the paraocular areas extremely reduced or absent (fig. 5). In the other families the laterofacial sutures may be rather close to the eye margins and largely parallel to them (many genera, *Amathusia, Calinaga, Leptidea, Papilio, Teinopalpus,* etc., see fig. 1) or they may be some distance from the eye margins and curved inward dorsally and ventrally (various nymphalids including *Danaus,* fig. 1—Pt. I). A complicating factor is that in some genera (*e.g., Calinaga,* fig. 1) the anterior tentorial pits do not lie at the juncture of the laterofacial and clypeolabral sutures as they do in *Danaus,* but rather at the free ends of the clypeolabral suture. In these genera the laterofacials pass laterad of the pits. Detailed studies of a great many different Lepidoptera as well as members of related orders will be necessary before we can

* Terminology after Clench, 1955.

hope to have a reasonable understanding of the structures of the face of the Lepidoptera.

In many Papilionidae and Lycaenidae the face is essentially flat (fig. 7) while in the other families it is at least somewhat protuberant. *Teinopalpus imperialis* (figs. 2, 3) has the entire frontoclypeal sclerite expanded into a balloonlike structure which accounts for about one half the total length of the head. Certain pierid genera (*Anthocharis, Leptidea, Pseudopontia,* etc.) also have very protuberant frontoclypeal sclerites. In most non-lycaenid genera the face is at least somewhat indented near the eye margins lateral to the frontoclypeal protuberance (fig. 2—Pt. I).

In most of the lycaenids the anterior tentorial pits are low on the face, usually about one seventh of the total height of the face from the lower margin of the labrum. In the other families the pits are somewhat higher.

The labrum of the butterflies is often difficult to define because of the obscurity of the clypeolabral suture. The labrum is greatly reduced in many genera (especially in the Lycaenidae—fig. 5). The pilifers are well developed in most groups, but are reduced or absent in some, including the Lycaenidae, *Baronia, Dismorphia, Lamproptera, Metamorpha, Pseudopontia,* and *Zerynthia.* The size and shape of the mandibular rudiment was also very variable, but it was difficult to describe the variation because of the indefinite boundaries of the rudiment. There is some variation in the depth of the proboscidial fossa (it is usually deeper in the Lycaenidae and Pieridae than in the other families), but it has not been systematically studied.

The maxillary palpi showed surprising development in some genera (including *Baronia, Caligo, Calinaga, Metamorpha* and *Pseudopontia*), being distinctly two-segmented in *Baronia.* The galeae of the maxillae are fringed with papillae at the distal end in *Actinote, Anaea, Apodemia, Atlides, Caligo, Calinaga, Heliconius, Libytheana, Lycaena, Lycaenopsis, Metamorpha, Morpho, Oeneis, Telipna* and many others. Numerous genera, principally papilionids, pierids and (to a lesser extent) nymphalids do not show this fringing or at least have the papillae greatly reduced. A detailed study of these structures would probably reveal taxonomic characters.

The labial palpi have been studied in great detail by Reuter (1897). The palps vary in length from as long as the thorax (some libytheids) to less than the length of the head (some papilionids and lycaenids). There is much variation in the proportions of the three segments and in the pattern of scaling and setation.

In the Nymphalidae, Libytheidae and Lycaenidae (except *Styx*) the labial sclerite is completely sclerotized, both in front of and behind the palpal sockets (figs. 3, 4—Pt. I). However, in most papilionids there is a loss of sclerotization in front of the sockets and in many pierids there is a loss of sclerotization behind the sockets.

On the vertex of the head there is a setiferous patch (presumably sensory) called the chaetosema. The variation in this organ is described and figured by Jordan (1923).

The anterior tentorial arms show a great deal of diversity. In some genera (*Apatura, Danaus, Heliconius, Historis, Ithomia, Leptidea,* etc.) they are relatively straight and simple (fig. 15), not greatly enlarged or downcurved anteriorly and not bearing crests. At the opposite extreme are genera such as *Lamproptera* and *Graphium* which bear extremely high dorsal crests (figs. 18, 19). In many genera, especially in the Lycaenidae, the arms are bent strongly downward anteriorly (fig. 17) and/or are more than twice as thick anteriorly as posteriorly.

CERVIX

In all of the Papilionidae studied (and in none of the other butterflies) the cervical sclerites were found to be joined beneath the neck by a narrow sclerotic band (fig. 24) which may be faint or slightly interrupted in the middle. Variation was observed in the shape of the cervical sclerites and in the position and shape of the cervical organ, but no study of this variation was made.

In *Lamproptera curius, Papilio machaon, Parnassius smintheus, Teinopalpus imperialis* and other papilionids as well as in *Apatura cyane* and *Historis odia* a small ventral sclerite was observed in the cervix close to the head (fig. 24). Among others it was absent from the following genera: *Actinote, Anaea, Apodemia, Atlides, Baronia, Caligo, Dismorphia, Fenesica, Ithomia, Leptidea, Libytheana, Lycaena, Lycaenopsis, Metamorpha, Pieris, and Phoebis.*

THORAX

Prothorax: In all the butterflies except the Pieridae the lateral plates of the pronotum fuse together to form a triangular or Y-shaped structure (fig. 8—Pt. I) which articulates with the dorsal plate. No such structure is found in the pierids (fig. 28). The dorsal plate itself may be roughly triangular, T-shaped, Y-shaped or sagittate.

Sclerotized patagia of varying size are found in all the Nymphalidae (fig. 37), the Coliadinae of the Pieridae (fig. 25), various

groups of the Papilionidae and the Libytheidae (fig. 26). In the libytheids and certain groups of the Papilionidae (Cressidini in particular) the sclerotized area is very small. All of the lycaenids, most of the pierids and a great many papilionids have the patagia unsclerotized. In some of these groups, particularly in certain lycaenids, the membranous patagia are rather prominent and protuberant, in others they are essentially indistinguishable from the rest of the membrane connecting the lateral plates of the pronotum with the mesothorax.

The Charaxinae of the Nymphalidae are the only butterflies in which sclerotized parapatagia have been found (fig. 37).

The presternum is generally present in the Nymphalidae, Libytheidae and Lycaenidae, although it is sometimes indistinctly separated from the ventrally fused propleura. It is absent in the Papilionidae and Pieridae.

The profurcal arms are simple (figs. 32, 33) in the Lycaenidae, Nymphalidae and Libytheidae. They usually have a secondary anterior lamella or prong in the Papilionidae and Pieridae (figs. 28, 29, 30, 31).

The intercoxal lamella is quite prominent (fig. 29) in the Pieridae and some Lycaenidae (*Atlides, Euselasia, Lycaena, Lycaenopsis, Megalopalpus, Telipna,* etc.). It is not prominent but present (fig. 33) in most of the Nymphalidae, the Libytheidae, and some Lycaenidae (*Apodemia, Fenesica,* etc.). In the Papilionidae the intercoxal lamella has migrated caudally, where it usually forms a prominent semicircular lamella almost between the furcal arms (fig. 30). In many of the papilionids (*Lamproptera, Papilio, Troides,* etc. but not *Parnassius, Teinopalpus,* etc.) and virtually all the pierids the discrimen is represented internally by a small anterior spine or lamella (figs. 29, 30).

In all the Papilionidae except *Baronia* the spinasternum is produced laterally at the spina (figs. 34, 35, 36). The process may be long (laterally visible, fig. 24) as in *Lamproptera, Papilio, Parnassius* and *Zerynthia* or short (not laterally visible) as in *Teinopalpus* and *Ornithoptera.* In most genera the processes are narrow; in *Zerynthia* they are broadened at the ends. In *Papilio* (at least some species) and *Lamproptera* there are areas of light sclerotization in the membrane around the processes, especially between the processes and the mesothoracic pre-episternum (fig. 34). Lateral processes of the spinasternum have not been found elsewhere in the butterflies.

In the vast majority of the Papilionoidea the spina is essentially

an invaginated sclerotized strip with membranous sides (figs. 8, 18—Pt. I). However, in a number of papilionids (*e.g., Ornithoptera priamus*), the spina is a tubular apodeme (completely sclerotized).

In the Nymphalidae, Libytheidae, and Lycaenidae the spinasternum is generally a narrow strip, invaginated at the spina, and gradually broadening caudally until it joins the thorax at two points with a membraneous triangle between them (fig. 17—Pt. I). However, in the Pieridae the spinasternum is widened into a small oval or diamond-shaped plate between the furcasternum and spina (fig. 31). This is faintly reminiscent of the lateral expansion of the papilionids.

In the Cressidini and *Ornithoptera* of the Papilionidae the spinasternum caudal to the spina is usually broad and platelike (figs. 35, 36).

Mesothorax: The prescutum of the Libytheidae is vertical to the main axis of the body or has its upper end slightly anterior to its lower end, giving the mesonotum a truncated appearance (fig. 26). This effect is also noticeable in a number of genera of lycaenids (*Apodemia, Euselasia, Fenesica, Lycaena, Lycaenopsis, Megalopalpus,* etc.). The remainder of the butterflies have the lower end of the prescutum anterior to the upper end and lack the truncated aspect (fig. 25).

In *Baronia* the scuto-scutellar suture is obsolescent, and in other genera such as *Leptidea, Lycaenopsis* and *Zerynthia* it is incomplete centrally.

The shape of the scuto-scutellar suture, especially the depth and angle of the inverted "V" is very variable but did not appear to have useful characters at the higher taxonomic levels.

The adnotale is sagittate in the Libytheidae (fig. 26); it is variable in shape but not sagittate in the other butterflies.

In general the processes of the second phragma are well developed. However, in many genera of the Lycaenidae (*Atlides, Euselasia, Lycaena, Lycaenopsis, Megalopalpus,* etc.) they are reduced to a greater or lesser degree.

In the sternopleural region of the butterflies there is a great amount of variation in the sutures and in the anepisternum.* The

* The nomenclature of the sternopleural region employed throughout this work has, as far as possible, been brought into line with the ideas of Matsuda (1956). Since the katapleuro-coxal muscle is absent from *Danaus* (and presumably from all butterflies due to the great degree of fusion of the coxae with the thorax proper) it has been impossible to identify with certainty the pleural costa. The choice of position of the pleural costa seems to lie between the pre-episternal and precoxal sutures (if indeed the pleural costa has not disappeared without a trace in the specialized lepidopterous thorax), and Matsuda agrees (personal communication) that considering the pre-episternal suture to be equivalent to the pleural costa gives the most satisfactory interpretation.

latter sclerite is present as a separate unit (figs. 37, 38, 39) in many papilionids (including *Baronia*); the Satyrinae, Morphinae, Calinaginae and Charaxinae of the Nymphalidae; the Styginae, Riodininae and a few Lycaeninae of the Lycaenidae. It is not present as a separate unit in the remainder of the butterflies (fig. 9—Pt. I).

There is a great deal of variation in the size and extent of the pre-episternum and the strength of the pre-episternal suture. The pre-episternum is about as wide as the katepisternum in *Anaea, Apodemia, Heliconius, Lycaenopsis, Megalopalpus, Speyeria* and many others. It is about one-half as wide as the katepisternum in a large number of genera (*Amathusia, Anthocharis, Caligo, Calinaga, Dismorphia, Morpho, Styx, Teinopalpus* [Fig. 38]) and is merely a narrow lip in a great many others such as *Actinote, Baronia, Danaus, Lamproptera, Papilio, Parnassius, Pieris, Phoebis, Pseudopontia,* etc. (fig. 24).

The greatest reduction of the pre-episternum is found in the nymphalid subfamilies Ithomiinae and Satyrinae, where it is sometimes essentially absent (fig. 39).

The pre-episternal suture varies from being absent in the Libytheidae (fig. 26) to being well developed with a strong internal ridge in a great many genera (*Actinote, Leptidea, Papilio, Parnassius, Pieris, Telipna,* etc.).

The precoxal suture is absent in the Papilioninae and Baroniinae of the Papilionidae and in the Pieridae. It is obsolescent or absent in the Libytheidae and in numerous genera of the Nymphalidae and Lycaenidae (*Actinote, Amathusia, Anaea, Apodemia, Atlides, Caligo, Fenesica, Lycaenopsis, Megalopalpus, Telipna,* etc.).

In some pierids the epimeron is fused to the meron, the suture which normally separates the two being absent anteriorly. The most extreme example of this is found in *Pseudopontia.*

In some genera, especially lycaenids, the marginopleurite (region between the marginopleural suture and eucoxa) is relatively wide (fig. 27). Some butterflies, especially Pieridae, have the discrimen forked (often broadly) at its anterior end.

The postcoxal sclerite is very variable in width and length. It is one half or more the width of the visible meron in caudal view (fig. 20—Pt. I) in *Actinote, Euselasia, Heliconius, Caligo, Danaus, Fenesica, Lamproptera, Libytheana, Lycaena, Metamorpha, Morpho, Oeneis, Speyeria* and many others. In *Dismorphia, Euselasia, Heliconius, Megalopalpus, Ornithoptera, Papilio, Parnassius* and others it is much less than one half the width of the visible meron.

In most genera the postcoxal sclerite ends well below the top of the meron (fig. 20—Pt. I); however, in many nymphalids (some Ithomiinae, some Satyrinae, some Nymphalinae, and all Morphinae, Calinaginae and Charaxinae) it is long (fig. 53), reaching the top of the meron.

Coxal sclerules were found only in the Danainae, *Historis* and *Ithomia.* They were absent in *Actinote, Anaea* (a trace present), *Apodemia, Caligo, Calinaga, Dismorphia, Euselasia, Fenesica, Lamproptera, Leptidea, Libytheana, Lycaenopsis, Megalopalpus, Metamorpha, Ornithoptera, Papilio, Phoebis, Pieris, Telipna* and many others.

The epimeron was found to be very variable, both in the presence of the pre-epimeron and various secondary sutures and ridges, but also in its height below the subalare in comparison with the epimeron-subalare distance. A systematic study of these features has not been made.

Another very variable character is the shape of the subalare. However, since the exact angle at which it is viewed is greatly responsible for its apparent shape, and since its position differs greatly from specimen to specimen this character was not used taxonomically.

Internally the principal variation studied was in the form of the lamella of the discrimen. The lamella is continuous with the furca (the dorsum of the lamella being essentially a straight line, fig. 40) in all the butterflies except the Lycaenidae and *Baronia* of the Papilionidae. In the Lycaenidae the lamella does not reach the furca, but instead curves downward to the base of the furca (fig. 42). The condition of the lamella in *Baronia* is intermediate (fig. 41).

A variable internal feature that was not studied in detail is the ventral process of the postalar portion of the epimeron. It varies both in length and in the shape of the end (conspicuously spatulate or more or less pointed).

Metathorax: In the Libytheidae the metanotum is almost completely covered by the mesoscutellum (fig. 26), being below it in position. In the other butterflies the metanotum is below and behind the mesoscutellum and is not completely covered by it (fig. 24).

The third phragma of most of the Papilionidae is in the form of paired simple lobes (fig. 55). In *Apatura, Caligo, Danaus, Morpho, Pieris* and others the phragma consists of paired stalked lobes (fig. 21—Pt. I). Most genera appear to be intermediate between the above conditions, having stalks but no lobes on their tips.

In the Libytheidae (fig. 26), *Fenesica, Zerynthia* and a few other forms the anepisternum is pointed ventrally to a greater or lesser degree. In the remainder of the butterflies it is rounded ventrally.

The relative size and position of the meron and eucoxa are subject to a great deal of variation. In *Dismorphia, Leptidea, Phoebis* and other pierids the meron is much larger than the eucoxa and arches high above it. In *Actinote, Caligo, Calinaga, Danaus, Historis, Libythea, Oeneis, Pieris, Pseudopontia* and many others the meron and eucoxa are of approximately equal size, but the former may arch above the latter to a variable extent. In general in the Lycaenidae the meron is somewhat larger than the eucoxa but does not arch high above it.

In the Papilionidae there is a transverse suture, represented internally by a lamella (the *meral suture* and *meral lamella*) crossing the meron (fig. 24). This suture is absent or indistinct in the rest of the butterflies.

The caudal part of the epimeron (beneath the base of the abdomen) varies from very thin (fig. 54) to very broad (fig. 55). Because it was a difficult character to quantify it was used very little in the taxonomic portion of this work.

In the vast majority of the butterflies the lamella of the metadiscrimen curves downward to the base of the furca. In certain Papilioninae, however, the lamella joins the furca above its base, and in *Pseudopontia* it runs straight into the furca as in the mesothorax.

LEGS

The various stages of reduction in size and fusion of segments in the prothoracic legs of butterflies are well known. It will suffice to say that the foreleg varies from a completely developed, full sized, functional appendage bearing tarsal claws and a tibial epiphysis (in the Papilionidae) to a vestigial appendage lacking both the tarsal claws and the epiphysis, in which the entire tibia and tarsus are reduced to a small ball at the end of the femur (certain Ithomiinae).

A rarely noted unique condition of the prothoracic leg of the Riodininae should be emphasized here. In this subfamily the coxa extends below the joint of the trochanter as a cylindroconical protuberance (fig. 57).

The pterothoracic tarsal claws of many butterflies are simple and symmetrical. However, they are strongly bifid in all the

Pieridae,* in *Lamproptera curius* (but not *L. meges*) and the *payeni* group of *Graphium* in the Papilionidae, in some Acraeinae, and in some Lycaenidae. The tarsal claws also tend to be asymmetrical in the Parnassiinae and Acraeinae.

Although most butterflies possess well-developed aroliar pads and pulvilli (the latter often bifid) on the pterothoracic legs, one or both of these are reduced or absent in the Papilionidae, *Baltia, Colias, Gonepteryx, Nathalis* and *Phulia* of the Pieridae, and certain Nymphalidae (*Acraea, Actinote, Agraulis, Euptoieta,* etc.).

WINGS

Most of the information in this work on wing venation has been taken from Schatz and Röber (1892), who illustrate the venation of some 480 genera of Papilionoidea.

The terminology "cubitus apparently trifid (or quadrifid)" has been adopted from Clench (1955). When M_2 of the forewing arises distinctly closer to M_3 than to M_1 and/or the vein connecting M_2 and M_3 appears to be a continuation of the vein connecting M_3 and Cu_1, then the cubitus is said to appear "quadrifid"—the four branches being actually M_2, M_3, Cu_1 and Cu_2. When M_2 arises midway between M_1 and M_3 or closer to the former, and/or the vein connecting M_2 and M_3 runs at a distinct angle to the vein connecting M_3 and Cu_1, then the cubitus is said to appear "trifid"—the three branches being M_3, Cu_1 and Cu_2.

It should be noted that the vein called cu-v in the Papilioninae is said to be a basal vestige of the first vannal vein.

ABDOMEN

Pregenital segments: The tergum of the first abdominal segment is strongly pouched in most butterflies. However, in some papilionids the amount of pouching is reduced. In a few groups (*Anaea, Caligo,* etc.) the first abdominal tergum is largely membranous.

The prespiracular bar is present in all groups except the Pieridae (fig. 25). The postspiracular bar is reduced (does not completely bridge membrane between tergum and sternum) or absent in the Papilionidae (fig. 24), Lycaenidae, and most Nymphalidae. Both bars are complete in some nymphalid genera (*Danaus, Ithomia, Metamorpha,* etc.) and in the Libytheidae (where the postspiracular bar is especially broad, fig. 26).

* In the Pieridae and Papilionidae the prothoracic legs share the characters of the pterothoracic legs, as do the prothoracic legs of the females of the Libytheidae and Lycaenidae.

There is considerable variation in the size and degree of sclerotization of the pregenital terga and sterna, but it has not been studied systematically.

There are occasionally special organs on the pregenital segments, such as pads bearing specialized scales on segments 4, 5, and 6 in *Caligo* and a deep pouch in the tergum of the second segment of *Faunis*.

Male genital segments: A number of species were found to have pseudovalves derived from the eighth tergum (*e. g., Parnassius smintheus*) or the eighth sternum (*e. g., Danaus plexippus*).

Variation of significance in the higher classification of the butterflies was found in the relative length of the tegumen and uncus; the presence or absence of a superuncus (fig. 62); the form of the uncus (simple or bifid); the form of the gnathos (complete, incomplete, absent), the form of the valvae (size as compared to the genitalia as a whole, thin or thick, dentate or smooth, etc.) and in the presence or absence of terminal hair brushes. The majority of the Lycaenidae possess genitalia with a more or less characteristic form (uncus not a pointed process, gnathos in the form of curved crossed arms, valvae reduced, etc.) but there was too much variation to merit employing these characters to differentiate the family.

Female genital segments: Although much variation is known to occur in these segments, especially in the lamellae ante- and postvaginalis and the bursa copulatrix, no study of this variation has been undertaken.

PHYLOGENY

Primitive and Specialized Characters

In order to make reasonable estimates of whether characters in a group studied are primitive or specialized it is usually necessary to have some knowledge of the state of the characters in the taxa presumed to be ancestoral to the group under consideration. Since almost certainly the "Protopapilionoidea" have become extinct, leaving no known fossil record, it is necessary to determine the primitive state of butterfly characters by inference from their states in various groups considered to be related to the butterflies. In order to do this a brief survey of the Lepidoptera has been carried out (see "Material and Methods" for list of non-papilionoids studied) with emphasis on groups which have been thought by various authors to be relatively closely allied to the butterflies (Hesperioidea; Castniidae; Cossidae; Tortricoidea, etc.). The

information obtained in this survey in combination with that gleaned from the literature (particularly Shepard, 1930, on the pterothorax; Schultz, 1914, on the pronotum and patagia; Weber, 1924, on the thorax; and Forbes, 1923, on venation, early stages, etc.) and from trends in the character within the butterflies themselves has been used to arrive at the judgments presented in Table I. In general any character state which was found to be widely distributed in the moths was considered to be primitive among the butterflies.

The development of some of the structures can be traced with ease and clarity from the primitive to the specialized state. The form of the lamella of the mesodiscrimen is such a character. In the neuropteroid insects (including Lepidoptera) there is probably no anterior sternal center of sclerotization in the thoracic segments, the anterior ventral sclerotizations in these segments consisting presumably of downgrowths from the pleural (coxal) regions. The line of fusion of these downgrowths is called the discrimen (Ferris, 1940). In the mesothorax (and to a lesser degree in the prothorax and metathorax) of the Lepidoptera this downgrowth seems to have continued, causing an invagination at the line of the discrimen and forming a thin internal "lamella of the discrimen." The lamella probably serves as a longitudinal strengthening device in the pterothoracic segments.

In the Hepialidae (which show a great many primitive characters—*i. e.*, characters shared by other orders of insects) the mesothoracic discriminal lamella is quite small. It is fairly strongly developed in the Cossidae and Castniidae and variable but usually rather weak in the Tortricidae, Yponomeutidae, Pyralididae and Thyrididae examined. In most of the higher moths, the skippers, and the lycaenids the lamella has reached the penultimate stage—high and strong but dipping completely to the base of the furca. In the remaining Papilionoids and in *Chrysiridia* (*leilus* but not *madagascariensis*) it has reached the highest stage of development, being complete to and fused with the furca. Weber (1924, fig. 3, a, b, and c) shows the progressive development of the lamella in *Hepialus, Zygaena* and *Papilio.*

In the above case the decision as to what is the primitive and what is the specialized case is relatively easy because of the morphologically logical sequence. In other cases the evidence is only slightly less conclusive. Sclerotized patagia are almost universal in their occurrence in the Lepidoptera; thus their absence in some members of an advanced group such as the papilionoids would

TABLE I—*Primitive and specialized characters in the Papilionoidea*

PRIMITIVE	SPECIALIZED
Eyes bare	Eyes hairy
Eyes entire	Eyes emarginate
Face at most moderately protuberant	Face extremely protuberant
Laterofacial sutures fairly close to eye margins	Laterofacial sutures far from eye margins or contiguous with them
Anterior tentorial arms simple, straight	Anterior tentorial arms crested, curved, etc.
Antennae approximately one-half to one scape width apart	Antennae much less than one-half or much more than one scape width apart
Antennae moderately long	Antennae very short or very long
Antennae scaled	Antennae unscaled
Pilifers conspicuous	Pilifers reduced or absent
Mandibular rudiments large *	Mandibular rudiments small
Maxillary palpi prominent, moveable, segmented	Maxillary palpi not prominent, immovable, unsegmented
Labial sclerite sclerotized all around palpal sockets *	Labial sclerite membranous either in front or behind sockets
Labial palps approximately twice length of head	Labial palps much longer or shorter than twice length of head
Cervical sclerites not joined	Cervical sclerites joined by a ventral sclerotic strip
No sclerotizations in cervix aside from cervical sclerites	A small anteroventral sclerite in cervix.
Patagia well sclerotized and large	Patagia not well sclerotized or small
Parapatagia well sclerotized and large	Parapatagia not well sclerotized or small
Lateral plates of pronotum fused dorsally into a Y-shaped or triangular structure.	Lateral plates of pronotum not fused dorsally into a Y-shaped or triangular structure
Presternum absent	Presternum present
Spine of prodiscrimen absent	Spine of prodiscrimen present
Profurcal arms simple	Profurcal arms with second anterior prong or lamella
Spinasternum not laterally produced	Spinasternum laterally produced
Spinasternum essentially an invaginated strip	Spinasternum a tubular apodeme
Pre-episternum of mesothorax broad	Pre-episternum of mesothorax narrow
Anepisternum of mesothorax a large, separate sclerite	Anepisternum of mesothorax reduced in size or not a separate sclerite
Precoxal suture present	Precoxal suture absent
Scuto-scutellar suture complete	Scuto-scutellar suture obsolete centrally
Metatergum not completely covered by mesotergum	Metatergum completely covered by mesotergum
Lamella of mesodiscrimen curved downward before furca	Lamella of mesodiscrimen complete to furca
Processes of second phragma small	Processes of second phragma large
Lamella of metadiscrimen curving downward to base of furca	Lamella of metadiscrimen not curving downward to base of furca
Third phragma in the form of lobes	Third phragma in the form of stalks or stalked lobes

* Judgment open to some doubt.

TABLE I—CONCLUDED

PRIMITIVE	SPECIALIZED
Dorsum of first abdominal tergum not pouched or weakly pouched	Dorsum of first abdominal tergum strongly pouched
Prespiracular bar present	Prespiracular bar absent
Postspiracular bar absent	Postspiracular bar present
Abdominal sclerites relatively large	Abdominal sclerites relatively small
Abdominal sclerites well sclerotized	Abdominal sclerites weakly sclerotized
Pseudovalves absent	Pseudovalves present
Tegumen well sclerotized	Tegumen membranous
Uncus a single, well sclerotized projection	Uncus bifid or weakly sclerotized
Arms of gnathos fused ventrally	Arms of gnathos not fused ventrally
Valvae large, broad, complete	Valvae reduced, narrow, simple
Sphragis absent	Sphragis present
Prothoracic legs normal size and functional	Prothoracic legs reduced in size, atrophied or not functional
Procoxae not extended to form a spinelike process below articulation with trochanter	Procoxae with spinelike cylindroconical projection below articulation with trochanter
Protibial epiphyses present	Protibial epiphyses absent
Tarsal claws symmetrical	Tarsal claws asymmetrical
Tarsal claws simple	Tarsal claws bifid
Aroliar pad present	Aroliar pad absent
Pulvilli present	Pulvilli absent
Tibial spurs present	Tibial spurs absent
Radius 5-branched	Radius 3- or 4-branched
Forewing with 2V and 3V free and running to margin	Forewing with 3V absent or fused after a short distance with 2V
Hindwing with 2V and 3V present	Hindwing with 3V lost
Wings with cell closed	Wings with cell open
Wings evenly rounded	Wings tailed, scalloped, angulate, falcate, etc.
Size moderate	Size extreme (very small or very large)
Body stout	Body slender
Flight powerful and rapid	Flight weak, fluttery
Dull colored	Brightly colored
Colors pigmentary only	Colors in part structural
Non-mimetic	Mimetic
Pupa with partial cocoon or girdle	Pupa without partial cocoon or girdle
Larvae herbivorous	Larvae carnivorous

seem almost certainly to represent a specialized loss rather than a primitive state.

The prespiracular bar of the butterflies was thought at first to be homologous with anterolateral apodemes found on the second abdominal sternite of many moths (including the Cossidae and Castniidae). The bar (presumably the homologue of the apodeme

lying in the membrane) was found in the butterflies, except the pierids where it is presumably lost, skippers, and a number of moths (*Thyris, Desmia, Peridroma,* etc.). *Catocala cerogama* shows a condition apparently transitional between apodeme and bar. However, in *Zygaena, Peridroma* and *Archips,* among others, both the bars and the apodemes are clearly present, making it certain that the two structures are not homologous. A trace of the apodeme can also be seen in *Thyris.* Interestingly in *Hepialus* there is no sign of either the apodeme or the prespiracular bar, but there is an extension of the first abdominal tergum which is very similar to the postspiracular bar. The question of which is primitive, bar or apodeme, will not be answered with real assurance until an exhaustive study of the moths is completed. In this work absence of the prespiracular bar is considered primitive in the Lepidoptera as a whole, but advanced within the Papilionoidea where it is lost in the Pieridae.

Similar problems have arisen in connection with other characters. Is the joining of the cervical sclerites of the Papilionidae by a ventral sclerotic band an adaptation from the primitive condition of the sclerites meeting at the center of the prothoracic "sternum" (*see* Weber, 1924, fig 1, c *[Hepialus]* and f *[Zygaena]*), or is it a secondary advanced condition, developed after the sclerites had become free? The latter alternative is chosen here since both sclerites are free in the Cossidae, Castniidae, Hesperiidae, and the majority of the moths.

In most cases, however, the decision as to which state of a character was primitive and which state specialized was relatively simple.

THE PAPILIONOIDEA AS A TAXON

There is little doubt that Papilionoidea is a monophyletic taxon. With the Hesperioidea (except for *Euschemon*) the Papilionoidea may be separated from the rest of the Lepidoptera by the combined loss of the frenulum and retinaculum and the possession of clubbed or distally swollen antennae. They may be separated from the hesperioids by the form of the head (discussed later). However, these distinctions could be considered somewhat superficial if they were not accompanied by certain trends, which help to characterize the Papilionoidea. It should be noted that these trends are not necessarily universal within the Papilionoidea or absent from all other Lepidoptera. Among the trends are: loss of ocelli; extreme atrophy of maxillary palps; loss of sclerotization of

labial sclerite; loss of sclerotized patagia; loss of sclerotized parapatagia; development of a presternum; reduction in the size of the prothoracic legs; fusion of segments in the prothoracic legs; loss of protibial epiphyses; loss of tibial spurs; simplification of the mesothoracic sternopleural region with loss of the precoxal suture and reduction of the anepisternum; development of a pair of prominent processes on the second phragma; extreme development of the lamella of the discrimen in the mesothorax and metathorax; development of stalks alone without lobes or stalked lobes instead of simple lobes of the third phragma; reduction, through fusion (including "stalking") and loss, of the number of wing veins; modification of wing shape (tails, scalloping, etc.); development of pre- and postspiracular bars; pouching of the first abdominal tergum; reduction and simplification of the valvae; development of relatively narrow thorax and long slender abdomen; reduction of scales and hairs (on thorax and antennae especially); upright egg; loss of use of silk at pupation; development of diurnal habits; development of brilliant pigmentary and structural colors.

It should be emphasized once again that the above, with very few exceptions, are only trends developed in the Papilionoidea, not diagnostic characters of the group.

RELATIONSHIPS OF THE PAPILIONOIDEA

Although any definitive statements on the relationships of the Papilionoidea with the remainder of the Lepidoptera will have to await a comprehensive study of the entire order, a few provisional observations are presented here.

Not surprisingly the Hesperioidea appear to be the closest living relatives of the papilionoids. With the exception of the male of *Euschemon,* which has a frenulum, the skippers all share the papilionoid diagnostic characters of the loss of the frenulum and the clubbed antennae. They are most readily separated from the papilionoids by the shape of the head, which is extremely wide in proportion to its height, and by the concomitant extreme separation of the bases of the antennae (the interantennal distance being at least twice the width of the scape). With rare exceptions the twelve veins of the primary wing of Hesperiidae (3V is vestigial or fused with 2V) all arise from the cell or wing base (*i. e.,* are "unstalked").

The best generalized morphological description of the hesperioids is that they appear to be papilionoids which possess a great many

primitive characters. Aside from the above-mentioned distinctions they differ from the papilionoids mainly in this concentration of primitive characters * in each species, not in the characters themselves. For instance all hesperioids examined retain the protibial epiphyses (in the papilionoids retained only in the Papilionidae); both sclerotized patagia and parapatagia (among papilionoids found in certain nymphalids only); lamella of discrimen curved downward before furca (lycaenids only); reduced but still relatively prominent mesothoracic anepisternum (retained in various butterfly groups) and stout body (retained in relatively few butterflies).

Not surprisingly the hesperioids have acquired some rather advanced characters, such as the extreme shape of the head, the trend towards stalks on the third phragma, the overhanging of the metanotum by the mesonotum (*Calpodes, Proteides*), and the "neck" of the larva.

It seems advisable at present to retain a separate superfamily for the skippers despite their obvious affinities with the papilionoids. It would be unwise to discard this well-accepted nomenclatorial practice without further study of the hesperioids.

The relationships of the butterflies with the various groups of moths is less clear, partially because of the difficulty of recognizing convergence without a more thorough knowledge of the moths. However, it seems evident that the direct ancestors of the Papilionoidea are no longer in existence. Aside from the Hesperioidea which are quite similar and closely related to the Papilionoidea, there are no groups showing clear evidence of intimate relationships to butterflies. There are, however, some groups which show a hint of papilionoid affinities, perhaps because of distant phyletic relationship.

The Castniidae are often mentioned as a possible papilionoid ancestor. It seems likely that these moths are a primitive offshoot of the line of Lepidoptera which leads eventually to the papilionoids. They possess clubbed antennae; a reasonable start, for so primitive a group, toward a lycaenid-type lamella of the mesodiscrimen; a strong, but low and unarched, lamella of the metadiscrimen; an upright egg; bright colors; and butterflylike habits. Most

* According to Yagi (1953) they are separated from the butterflies by having eyes of the superposition type. This is a most interesting character, if substantiated, since this type of eye is characteristic of nocturnal insects and is designed for maximum utilization of available light. The skippers are fully as diurnal as the butterflies. However, Yagi further states that the eye is functionally of the apposition type, because the shape of the crystalline cone causes the light passing through it to be concentrated on the end of the rhabdome, rather than allowing it to pass on to other ommatidia.

of the other characters of the group are primitive and not particularly associated with the papilionoid line (*e. g.*, ocelli usually present; tentorial bridge "inside" of head rather than at the foramen magnum; large mesothoracic anepisternum; venation complex, etc.).

The cossid studied showed a slight reduction in the size of the mesothoracic anepisternum. Aside from this and the possession by the members of the subfamily Cossinae of an upright egg, there is little to connect the Cossidae with the papilionids.

None of the species of tortricoids, pyraloids, yponomeutoids, etc. studied showed any combination of characters to suggest that they are crucial to the matter at hand. They are doubtless more closely related to the butterflies than some of the more specialized moths such as the saturnoids, but beyond this little can be said.

In summary, the evidence seems to indicate that the butterflies and skippers are highly evolved representatives of a line which is well isolated from all other living Lepidoptera.

INTERRELATIONSHIPS OF THE FAMILIES OF THE PAPILIONOIDEA

Of the five families of butterflies only two pairs can be associated with any degree of certainty as being more closely related to each other than to the other families. These are the Papilionidae and Pieridae and the Nymphalidae and Libytheidae.

The classical character which associates the papilionids and pierids is the complete development of the prothoracic legs. Accompanying this is the similar trend in the development of the patagia, the absence of the presternum, the loss of the precoxal suture, the similarities in the profurca and prodiscrimen, the general similarity of the head structure (including a tendency towards loss of sclerotization in the labial sclerite) and the general tendency towards broadening of the spinasternum.* The quadrifid cubitus which is characteristic of the Papilionidae is found also in the Dismorphiinae of the Pieridae (and nowhere else in the butterflies). The bifid tarsal claws which are universal in the Pieridae are found also in a few papilionids as well as in certain nymphalids and lycaenids. *Hypermnestra helios* is a papilionid which has facies very similar to those of certain pierids (*Euchloe sp.*).† Some workers have associated the Pieridae with the Lycaenidae rather than the Papilionidae, but the great mass of evidence is against this. The

* The above characters are discussed in detail in the section on comparative morphology and in the family diagnoses.

† The investigations of Homma (1954) on the alimentary canals of butterflies, although relatively incomplete, tend to support the systematic relationships put forth in the present work. Homma states, "The externals of the canal of Papilionidae are somewhat similar to those of Pieridae, and those of Nymphalidae closely resemble those of Satyridae."

Pieridae differ from the Lycaenidae in almost every character of the head, in the development of the prothoracic legs, in almost every character of the prothorax, in most of the characters of the mesothorax (including the form of the lamella of the discrimen) and in the development of the prespiracular and postspiracular bars and male genitalia.

The Libytheidae share so many characters with the Nymphalidae that very serious consideration was given to including them in the Nymphalidae as a subfamily.

The libytheids differ from the nymphalids in having almost completely developed prothoracic legs in the females, only small sclerotic areas on the patagia, and the metanotum almost completely beneath the mesoscutellum. The long labial palpi usually associated with the Libytheidae are short enough in some species to cause overlap with the length of the palpi of some nymphalid genera. A number of other characters which are typical of the Libytheidae also can be found within the nymphalids so that they cannot be considered diagnostic.

One other entity, the Baroniinae, was considered to be of possible family rank. *Baronia* differs from the rest of the papilionids in (among other characters) not having the spinasternum laterally produced (some other papilionids have it only slightly produced), in having a well-developed second vannal vein in the hindwing (absent or rudimentary in the other papilionids), and in having the lamella of the mesodiscrimen curved downward before it joins the furca (a condition unique in the butterflies). In this case it was decided to retain the Baroniinae as a subfamily, since these differences did not seem as great as those separating the Nymphalidae and Libytheidae.*

As stated earlier it does not seem wise to place labels of "primitive" or "specialized" on groups as closely related as the families of butterflies. However, as a matter of interest, the distribution among families of 36 characters for which the primitive and specialized states had been hypothesized was studied. Each character was rated for each family on a scale from 0 to 5, 0 indicating that the character was found throughout the family in its most primitive state and 5 indicating that it was found throughout the family in its most specialized state. Both intermediate states of the characters and their distributions within the families were considered in estimating the intermediate values. A family possessing all the

* Necessarily a partly subjective decision.

characters in their most specialized state in all its members would then score 180 points. The sums of the figures were determined for each family and then divided by 180 and multiplied by 100 so that they were expressed as a percentage of the maximum score. The results were: Papilionidae—53%; Pieridae—42%; Nymphalidae —42%; Libytheidae—37%; Lycaenidae—43%. Considering the crudity of the method the only conclusion which is drawn from these data is that there is certainly no indication that the Papilionidae are "primitive" as has been claimed (largely because of the completely developed prothoracic legs and presence of the epiphyses). Indeed this method showed them to have the highest percent of specialized characters of any family.

Figure 64 is a diagram giving the author's ideas on the phyletic relationships of the families and subfamilies of the Papilionoidea. The reasons for the arrangement of the various branches are discussed in this section and under the various families in the following section. The vertical scale is my judgment of what might be called evolutionary distance, being evolutionary rate multiplied by time. It is, of course, impossible to distinguish these two quantities on the basis of neozoological evidence. The horizontal positions of the taxa and spacing of the lines are determined by convenience.

CLASSIFICATION

KEY TO THE FAMILIES OF THE PAPILIONOIDEA*

1. Lamella of mesodiscrimen continuous with furca, dorsum of the lamella essentially straight (somewhat downcurved in *Baronia*); eyes not emarginate; patagia either sclerotized or unsclerotized 2

   Lamella of mesodiscrimen not continuous with furca, curving downward to base of furca; eyes usually emarginate; patagia unsclerotized ..... Lycaenidae

2. Cervical sclerites not joined beneath cervix; epiphyses absent; hindwing with two distinct vannal veins 3

   Cervical sclerites joined or nearly joined by a sclerotic band beneath cervix; epiphyses present; hindwing with only one distinct vannal vein (two in *Baronia*) ..... Papilionidae

3. Prespiracular bar well developed; prothoracic legs atrophied (smaller than the pterothoracic legs) to some degree (only slightly in females of Libytheidae); tarsal claws very rarely strongly bifid 4

* Since butterfly specimens have always been, and will continue to be identified by comparison of facies and genitalia with illustrations, no attempt has been made to construct superficial keys. This key and those that follow are based on what appear to be the most dependable characters, regardless of accessibility. Wherever possible they have been designed to be used with adults of either sex. They will probably prove most useful in placing new or little known forms.

Prespiracular bar reduced or absent, prothoracic legs fully developed (as large as pterothoracic legs); tarsal claws always strongly bifid ..... Pieridae

4. Patagia prominent, rounded, sclerotized structures; metanotum not entirely below mesoscutellum, only partially covered by it, Nymphalidae

Patagia not prominent or rounded, bearing only small lateral sclerotizations; metanotum essentially entirely below mesoscutellum, covered by it ..... Libytheidae

FAMILY PAPILIONIDAE

1) Eyes entire; 2) eyes bare; 3) face at least somewhat protuberant; 4) laterofacial sutures seperated from eye margins; 5) paraocular areas relatively small (fig. 1); 6) antennae close together to widely separated; 7) anterior tentorial pits high on face; 8) proboscidial fossa shallow; 9) labial palps much shorter than thorax; 10) labial sclerite well sclerotized only behind palpal sockets, not extended liplike beneath cervix; 11) anterior tentorial arms greatly enlarged anteriorly, but not strongly downcurved (fig. 23), sometimes bearing crests (figs. 18, 19, 20, 21) which may be very high; 12) antennae not carinate; 13) cervical sclerites united beneath neck by a narrow sclerotic band (which is sometimes weak or broken at center); 14) dorsal plate of pronotum sagittate; 15) spinasternum laterally produced to a greater or lesser degree at the spina (except in *Baronia*); 16) profurcal arms with secondary anterior prong or lamella (fig. 30) except in *Baronia;* 17) intercoxal lamella and lamella of prodiscrimen variable; 18) lateral plates of pronotum fused dorsally into a Y-shaped or triangular structure; 19) patagia membranous or with relatively small elongate sclerotic areas; 20) parapatagia membranous; 21) presternum absent; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca (curved downward somewhat in *Baronia*); 24) processes of second phragma prominent; 25) precoxal suture absent (except in Parnassiinae); 26) pre-episternum of mesothorax narrow (except in *Teinopalpus*); 27) mesothoracic anepisternum variable in character, often a separate sclerite; 28) prescutum not vertical; 29) meral suture and lamella present and prominent (except in *Parnassius* and *Baronia*); 30) third phragma consisting of simple lobes (fig. 55); 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron variable in width; 33) prespiracular bar fully developed; 34) postspiracular bar reduced or absent; 35) cubitus of forewing apparently quadrifid; 36) 3V of forewing present and running to inner margin; 37) hindwing with only one well-developed vannal vein (two in *Baronia*); 38) pro-

thoracic legs fully developed in both sexes; 39) protibiae bearing epiphyses (fig. 56); 40) tarsal claws simple (except in *Lamproptera curius* and the *payeni* group of *Graphium*); 41) aroliar pad and pulvilli absent or reduced; 42) pupa with girdle (except in *Parnassius*, modified in *Zerynthia*); 43) larva with osmateria.

The most recent work on the classification and evolution of the Papilionidae is that of Ford (1944). Unfortunately so many of the conclusions arrived at in the present work are diametrically opposed to those of Ford that a detailed discussion of the problems involved and the points of difference seems necessary.

Perhaps the greatest differences center around the concepts of primitive and specialized species and characters. As stated in the introduction it would appear to be dangerous to label entities as "primitive" or "specialized" unless one is dealing with considerable systematic distance, and even in this case the terms should be used with reservation. In a group as uniform as the Papilionidae assigning these labels to species, genera, or subfamilies is in all likelihood biologically meaningless. However, there is nothing wrong with attempting to label character states in the family as primitive or specialized as long as one is willing to admit ignorance when the data will not permit a decision to be made.

Ford states (p. 210) that "the presence of a tail, supported by vein 4 of the hindwings, must be regarded as an ancestral characteristic of the family." There is little doubt that tails have been lost secondarily in many of the species of *Papilio* (*s. l.*). However, if Ford is correct, then the ancestral papilionid must have developed a tail, which has then been independently lost in *Baronia* and the Parnassiini as well as in *Zerynthia*. The alternative hypothesis is that the possession of tails is an advanced character which has not been developed in *Baronia* or the Parnassiini, and is being developed in *Zerynthia*. For want of evidence to settle the question we are bound by the rule of parsimony to consider seriously the latter hypothesis.

Again, Ford concludes that short palpi are "doubtless" primitive in the Papilionidae "for they are long only in the somewhat specialized Zerynthiinae and in the highly specialized *Teinopalpus*, in which latter they are produced to an extravagant degree." Considering the shape of the head, the palps of *Teinopalpus* are not at all extravagant. The palps are also not extremely short in the Parnassiini. Once again parsimony would have us select palps of "normal" length as primitive in the family, rather than the extremely reduced palps of *Baronia* and most *Papilioninae*.

The sphragis or "female pouch" is of such sporadic occurrence in the family that it would seem wise to exclude it from phylogenetic discussion except to say that the tendency to possess it is an advanced character of the family as a whole. Ford considers the sphragis to be primitive in the family and vestigial in *Parides* (= *Atrophaneura*) *proneus* Hübner (and in certain other neotropical species of *Parides* where it also occurs).

Ford's very interesting pigment characters have been employed by him with proper restraint, but once again his reasoning about their primitive and specialized states is inconclusive if not incorrect.

Key to the subfamilies and tribes of the Papilionidae

1. Forewing with vein cu-v absent or (rarely) vestigial, if vestigial face not extremely protuberant; male with tarsal claws usually asymmetrical, females with tarsal claws sometimes asymmetrical 2
   Forewing with vein cu-v complete or (rarely) vestigial, if vestigial face extremely protuberant; tarsal claws symmetrical, Papilioninae 4
2. Hindwing with two distinct vannal veins; spinasternum not produced laterally at spina; tarsal claws symmetrical. . Baroniinae
   Hindwing with only one distinct vannal vein; spinasternum produced laterally at least to some extent; tarsal claws usually asymmetrical in males, sometimes in females. . . . Parnassiinae 3
3. Antennae unscaled; labial palps more than twice length of head; margin of hindwing scalloped or with tails; radius 5-branched, Zerynthiini
   Antennae scaled; labial palps less than twice length of head; margin of hindwing smooth; radius 4-branched (except in *Archon*) ..... Parnassiini
4. Face extremely protuberant; cu-v cross vein of forewing vestigial, Teinopalpini
   Face not extremely protuberant; cu-v cross vein of forewing not vestigial 5
5. Patagia membranous ..... Papilionini
   Patagia each with at least a small sclerotic area 6
6. Patagia with strong, fairly large sclerotizations; anterior tentorial arms with very high crests (figs. 18, 19) ..... Graphiini
   Patagia with weak, small sclerotizations; anterior tentorial arms with medium sized crests (figs. 20, 21) ..... Cressidini

Papilioninae

a) Antennae close together to far apart; b) labial palps very short, approximately as long as head (somewhat longer in *Teinopalpus*); c) tentorial arms with or without prominent crests; d) patagia membranous or sclerotized; e) spinasternum laterally produced at spina; f) profurcal arms with second anterior prong or lamella;

g) intercoxal lamella prominent and caudad of its usual position in the butterflies; h) prodiscrimen often represented by a prominent anterior spine; i) lamella of mesodiscrimen not curved downward before furca; j) precoxal suture absent; k) meral suture and lamella prominent; l) lamella of metadiscrimen curved downward to base of furca or complete to furca; m) forewing with vein cu-v complete (except in *Teinopalpus*), radius 5-branched; n) hindwing with one well-developed vannal vein; o) tarsal claws symmetrical, simple in all except *Lamproptera curius* and the *payeni* group of *Graphium* in which they are bifid; p) pupa without a cocoon.

World-wide in distribution but mainly tropical. Greatest morphological diversity found in Old World tropics.

Genera examined: *Battus, Cressida, Euryades, Graphium, Lamproptera* (= *Leptocircus,*) *Ornithoptera, Papilio, Parides* (= *Atrophaneura*), *Teinopalpus, Trogonoptera*, Troides.*

In order to save the reader the trouble of referring constantly to Table I, a (P) or an (S) will be placed after each character state mentioned in the following discussion to show whether it is considered to be primitive or specialized.

The Papilioninae are provisionally divided into four tribes, three of which contain fragments of the old polyphyletic genus *Papilio.* The tribe Graphiini contains at present two genera, *Graphium* and *Lamproptera.* Aside from the more classical characters which relate these two genera, they both possess highly crested anterior tentorial arms (S) (figs. 18, 19), a narrow spinasternum (P), well-sclerotized patagia (for the Papilionidae) (P), a lamella of the metadiscrimen which is curved downward to the base of the furca (P), and a tendency towards bifid tarsal claws (S). They both lack the spine of the prodiscrimen (P). Ford's statement that the Graphiini "must have been derived from some ancestral stock within the Troidini" is probably incorrect. Of course, the two share at some point a common ancestor, but all the genera placed by Ford in the "Troidini" (*Battus, Troides, Parides*) either have patagia which are membranous or at most possess very small sclerotizations. In order for the Graphiini to be derived from one of these genera the sclerotizations would have to have been reduced or lost and then regained.

The tribe Cressidini contains three genera, the small, very closely related *Cressida* (1 species) and *Euryades* (2 species), and the large, widespread *Parides.* In these genera the tentorial arms have medium-sized crests (S), the spinasternum is usually quite broad

* Not dissected.

posteriorly, often with parallel sides (S) (figs. 35, 36), the patagia have very reduced sclerotizations (S), the lamella of the metadiscrimen is not curved downward to the base of the furca (S) and the tarsal claws are simple (P). These genera all possess the spine of the prodiscrimen (S) (fig. 30).

The tribe Papilionini contains the various ornithopteran genera as well as *Papilio* and *Battus*. In these genera the tentorial arms either have medium-sized (S) or very reduced crests (P), the spinasternum is either narrow (P) (fig. 34) or widened (S) (fig. 35), the patagia are completely membranous (S), the lamella of the metadiscrimen may (P) or may not (S) curve downward to the base of the furca. The tarsal claws are simple and the spine of the prodiscrimen may (S) or may not (P) be present. This heterogeneous tribe needs considerable additional study. It is quite possibly polyphyletic. *Ornithoptera* and *Troides* share the broadened spinasternum with the genera of the Cressidini and may actually be more closely related to them than to *Papilio*.

The final tribe of the Papilioninae is the Teinopalpini, with one genus, *Teinopalpus* (1 or 2 species). The tribe is characterized by the unique expansion of the frontal area of the head (S) (figs. 2, 3) and a correlated elongation of the palpi (S), by highly crested tentorial arms (S), membranous patagia (S), presence of the spine of the prodiscrimen (S), a narrow spinasternum (P), a lamella of the metadiscrimen which curves downward to the base of the furca (P), and simple tarsal claws (P).

Parnassiinae

a) Antennae close together (separated by less than one half width of scape); b) labial palps longer than head; c) tentorial arms crested; d) patagia membranous or sclerotized; e) spinasternum laterally produced at spina; f) profurcal arms with second anterior prong or lamella; g) intercoxal lamella prominent, and somewhat caudad of its usual position in the butterflies; h) prodiscrimen not represented anteriorly by a spine; i) lamella of mesodiscrimen not curved downward before furca; j) at least a trace of precoxal suture present; k) meral suture and lamella varying in prominence; l) lamella of metadiscrimen curved downward to base of furca; m) forewing lacking vein cu-v, radius 4- or 5-branched; n) hindwing with one well-developed vannal vein; o) tarsal claws usually asymmetrical, always simple; p) pupa with or without cocoon.

Holarctic and oriental with greatest diversity in Asia.

Genera examined: *Archon, Bhutanitis, Hypermnestra, Leudorfia, Parnassius, Sericinus, Zerynthia.*

The Parnassiinae are divided into two tribes, Parnassiini and Zerynthiini. These entities are considered to be of subfamily rank by Ford, and there is some justification for this view. *Parnassius, Archon,* and *Hypermnestra* form a very closely knit group, sharing among other things an unusual type of pupa (S), scaled antennae (P), and relatively well-developed patagia (P). *Archon* differs from the other two genera in having a 5-branched radius (P), and *Hypermnestra* differs from the others in having nearly symmetrical tarsal claws in both sexes (there are reports of *Parnassius* species in which the males have nearly symmetrical claws, but Schatz and Röber [1892] are in error when they illustrate this condition for *P. apollo* L.). All three genera of the Parnassiini lack any hint of tails on the hindwing (P).

The Zerynthiini differ from the Parnassiini in possessing bare antennae (S), and hindwings which are either scalloped or tailed (S). The pupa is not formed in a cocoon as in the Parnassiini and (except in *Leudorfia*) the patagia are not very well sclerotized (S). The radius is universally 5-branched (P), differing in this respect from all the Parnassiini except *Archon.* In both tribes the labial palpi are much longer (P) than in the Papilioninae or Baroniinae, but they are shorter in the Parnassiini than in the Zerynthiini.

As can be seen from the above the Parnassiinae divides rather clearly into two tribes which could be raised to the rank of subfamily. However, considering the types of differences found between the tribes of the Papilioninae, it would appear that the level of difference between the Parnassiini and Zerynthiini, within the nomenclatorial structure used in this paper, is tribal rather than subfamilial. No reason can be found for placing these two tribes at opposite sides of a diagram of relationships as has been done by Ford (1944). Indeed, even after accepting without question all of the assumptions which he has employed as a basis for the diagram, it is difficult to find justification for this. For the characters shared by the Parnassiini and Zerynthiini the reader is referred to the subfamily diagnosis.*

Baroniinae

a) Antennae close together (separated by less than one half width of scape); b) labial palps very short, approximately as long as head; c) tentorial arms somewhat crested (fig. 22); d) patagia with relatively small, elongate sclerotizations; e) spinasternum not laterally produced at spina; f) profurcal arms simple; g) intercoxal

* Homma's (1954) work on the alimentary canal places *Luedorfia* (the only Zerynthiini which he studied) very close to *Parnassius.*

lamella prominent, not caudad of its usual position in the butterflies; h) prodiscrimen not represented anteriorly by a spine; i) lamella of mesodiscrimen curved downward somewhat at furca (not to base); j) precoxal suture absent; k) meral suture and lamella ventral and not prominent; l) lamella of metadiscrimen curved downward to base of furca; m) forewing lacking vein cu-v, radius 4-branched; n) hindwing with two well-developed vannal veins; o) tarsal claws symmetrical, simple; p) pupa unknown.

Represented by a single monobasic genus from southwestern Mexico.

Genus examined: *Baronia.*

Family Pieridae

1) Eyes entire; 2) eyes bare; 3) face at least somewhat protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small (fig. 1); 6) antennae widely separated (more than one half scape width apart); 7) anterior tentorial pits high on face; 8) proboscidial fossa shallow or deep; 9) labial palps much shorter than thorax; 10) labial sclerite usually well-sclerotized only in front of palpal sockets, rarely extended liplike below cervix; 11) form of anterior tentorial arms variable (not highly crested); 12) antennae not carinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina but slightly enlarged in front of spina into an oval or diamond-shaped plate; 16) profurcal arms with secondary anterior prong (figs. 28, 29, 31) (except in *Pseudopontia*); 17) intercoxal lamella prominent, prodiscrimen represented anteriorly by a second small lamella or spine (fig. 29); 18) lateral plates of pronotum fused dorsally but not forming a Y-shaped or triangular structure (fig. 28); 19) patagia membranous or sclerotized; 20) parapatagia membranous; 21) presternum absent; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture absent; 26) pre-episternum of mesothorax narrow to one half size of katepisternum; 27) mesothoracic anepisternum not present as a separate sclerite; 28) prescutum not vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma variable in character; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron thin (fig. 54); 33) prespiracular bar greatly reduced or absent (fig. 25); 34) postspiracular bar normal; 35) cubitus of forewing appears either quadrifid

or trifid; 36) 3V of forewing when present fusing with 2V, not running to inner margin; 37) hindwing with two well-developed vannal veins; 38) prothoracic legs fully developed in both sexes; 39) protibial epiphyses absent; 40) tarsal claws strongly bifid; 41) aroliar pad and pulvilli usually present; 42) pupa with girdle; 43) larvae lacking osmateria.

Key to the Subfamilies of the Pieridae

1. Forewing with M_2 arising from end of cell; hindwing with $Sc + R_1$ not secondarily fused with R_s; hindwing with M_2 arising from cell 2
   Forewing with M_2 stalked with R_{3+4+5}; hindwing with $Sc + R_1$ secondarily fused with R_s before middle of wing; hindwing with M_2 stalked with M_1 ..... Pseudopontiinae
2. Forewing with 3 to 5 radials present, at least one arising from the cell; forewing with cubitus appearing trifid 3
   Forewing with 5 radials present, all stalked; forewing with cubitus appearing quadrifid ..... Dismorphiinae
3. Patagia unsclerotized; humeral vein usually long; tegumen longer than uncus ..... Pierinae
   Patagia sclerotized; humeral vein usually greatly reduced or absent; tegumen usually considerably shorter than uncus, Coliadinae

Pseudopontiinae

a) Patagia unsclerotized; b) forewing with three radial veins; c) forewing with all radial veins arising from cell; d) forewing with M_2 stalked with R_{3+4+5}; e) forewing with cubitus apparently trifid; f) hindwing with humeral vein well developed; g) hindwing with $Sc + R_1$ secondarily fused with R_s before middle of wing; h) hindwing with M_2 stalked with M_1; i) tegumen extremely reduced, much shorter than uncus; j) uncus reduced to two small lobes, one on either side of anus; k) valvae fused together along ventral and lower distal margins.

Represented by a single monobasic genus from West Equatorial Africa.

Genus examined: *Pseudopontia.*

Dismorphiinae

a) Patagia unsclerotized; b) forewing with five radial veins; c) forewing with all radial veins stalked; d) forewing with M_2 arising from cell; e) forewing with cubitus apparently quadrifid; f) hindwing with humeral vein well developed; g) hindwing with $Sc + R_1$ not secondarily fused with R_s; h) hindwing with M_2 arising from cell; i) tegumen reduced, much shorter than uncus;

j) uncus well developed, bilobed; k) valvae fused together along ventral and lower distal margins.

Primarily neotropical but with one small palearctic genus (*Leptidia*).

Genera examined: *Dismorphia, Leptidia, Pseudopieris.*

Pierinae

a) Patagia unsclerotized; b) forewing with three to five radial veins; c) forewing with at least one radial vein arising from cell; d) forewing with M_2 arising from cell; e) forewing with cubitus apparently trifid; f) hindwing with humeral vein usually well developed; g) hindwing with Sc + R_1 not secondarily fused with R_s; h) hindwing with M_2 arising from cell; i) tegumen not reduced, longer than uncus; j) uncus well developed, simple; k) valvae not fused together.

Cosmopolitan, reaching greatest variety in the tropics.

Genera examined: *Anthocharis, Aporia, Appias, Archonias, Belenois, Cepora, Colotis, Delias, Dixeia, Euchloe, Hebomoia, Itaballia, Ixias, Leptophobia, Leptosia, Melete, Neophasia, Pereute, Perrhybris, Pieris, Prioneris, Zegris.*

Coliadinae

a) Patagia sclerotized; b) forewing with three to five radial veins; c) forewing with at least one radial vein arising from cell; d) forewing with M_2 rising from cell; e) forewing with cubitus appearing trifid; f) hindwing with humeral vein usually reduced or absent; g) hindwing with Sc + R_1 not secondarily fused with R_s; h) hindwing with M_2 arising from cell; i) tegumen not extremely reduced, but usually considerably shorter than uncus; j) uncus well developed, simple; k) valvae not fused together.

Cosmopolitan, reaching greatest variety in the tropics.

Genera examined: *Anteos, Colias, Eurema, Gonepteryx, Kricogonia, Leucidea, Nathalis, Phoebis, Zerene.*

The subfamilial classification of the Pieridae adopted in this work is based principally on Klots' (1933) generic revision of the family. The only major change is the elevation of Klots' tribe "Rhodocerini" to subfamily status (Coliadinae), a change which has been made previously by other authors (*e. g.*, Ford, 1945). The discovery of the consistent differences in the patagia (involving even such atypical appearing "yellows" as *Leucidia*) seemed to favor giving the group subfamily status.

FAMILY NYMPHALIDAE

1) Eyes entire; 2) eyes bare or hairy; 3) face at least somewhat protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small (fig. 1) to large (fig. 1—Pt. I); 6) antennae close together to widely separated; 7) anterior tentorial pits high on face; 8) proboscidial fossa usually shallow; 9) labial palps much shorter than thorax; 10) labial sclerite well sclerotized all around palpal sockets, rarely extended liplike below cervix; 11) form of anterior tentorial arms variable; 12) antennae almost always tricarinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella not prominent, or absent; 18) lateral plates of pronotum fused dorsally forming a Y-shaped or triangular structure (fig. 8—Pt. I); 19) patagia prominent, well sclerotized (fig. 37); 20) parapatagia membranous or sclerotized; 21) presternum present; 22) adnotale not sagittate; 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture usually present, with varying inflection; 26) pre-episternum of mesothorax narrow or essentially absent to one half magnitude of katepisternum; 27) mesothoracic anepisternum often present as a separate sclerite; 28) prescutum usually not vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma very variable in form but not consisting of simple lobes; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron intermediate between thin and broad in width to broad (never thin); 33) prespiracular bar fully developed; 34) postspiracular bar variable in development; 35) cubitus of forewing appears trifid; 36) 3V of forewing, when present, fusing with 2V, not running to inner margin; 37) hindwing with two well-developed vannal veins; 38) prothoracic legs atrophied in both sexes, clawless (except in *Calinagà* and some Ithomiinae in which there are small claws in the females); 39) protibial epiphyses absent; 40) tarsal claws usually simple (bifid in some acraeines); 41) aroliar pad usually well-developed, pulvilli usually large and bifid; 42) pupa without girdle; 43) larva without osmateria.

Because of the tremendous diversity of appearance found in the vast assemblage of the nymphalids, the Nymphalidae (*s. l.*) have been previously broken up into a large number of families and subfamilies. Clark (1948) recognized eight families and

twenty-three subfamilies in the group "Nymphalides" (excluding Libytheidae which he erroneously placed with the lycaenids).

Morphologically the Nymphalidae are a comparatively uniform group in spite of the large number of genera and species included. In general, the differences between the subfamilies outlined below are equivalent (insofar as it is possible to equate them) to those found between tribes or genera of the Papilionidae. The variation which does exist is in many cases continuous, leaving few obvious gaps at which to establish subfamilial limits. Likewise discontinuities in the variation of one character often do not coincide with discontinuities in the variation of others. In spite of these difficulties, several distinct lines of evolution may be detected within the group (see diagram of relationships—fig. 64).

One line includes the Ithomiinae and Danainae. Both of these subfamilies have lost the separate mesothoracic anepisternum (S) *, have a pronounced caudal bulge of the mesomeron (found only in these two subfamilies) (S), have the base of vein 3V free in the forewing (P), and have the forewing and hindwing discal cells closed by tubular veins (P). Also certain ithomiines show reduction of the female protarsus to the 4-segmented condition (S) found universally in the danaines.

Four subfamilies of the Nymphalidae (Satyrinae, Morphinae, Calinaginae, Charaxinae) have retained the mesothoracic anepisternum as a separate sclerite. Two of these, Satyrinae and Morphinae appear to be quite closely related. Both groups have rather simplified dentate valvae (S) (a few exceptions in the Morphinae), the discal cell of the forewing closed (P), a tendency towards closure of the discal cell of the hindwing (P) (all satyrines and most morphines), larvae with bifid tails (S) and monocotyledonous foodplants (all except *Morpho*) (S?). The Satyrinae and Morphinae both usually have prominent eye-spots in the pattern.

The monobasic subfamily Calinaginae is apparently allied to the satyrines and morphines, having the cells of both wings closed by relatively thick veins. Unfortunately its early stages are unknown.

The subfamily Charaxinae is somewhat anomalous. In almost all characters except the condition of the anepisternum and parapatagia it appears to belong with the Nymphalinae.†

* (S) signifies a character believed to be specialized, (P) primitive.

† The genus *Stibochiona* of the Nymphalinae also has sclerotized parapatagia.

The Nymphalinae and Acraeinae are connected by a series of nymphaline genera sometimes segregated as the subfamily "Heliconiinae" (*Heliconius, Eueides, Dryas, Dryadula, Dione, Agraulis, Philaethria*). Both subfamilies lack the separate anepisternum, and with minor exceptions have no trace of vein 3V at the base of the forewing. The aroliar pads of the pterothoracic tarsi are lost in some genera of each subfamily (S).

Key to the Subfamilies of the Nymphalidae

1. Mesothoracic anepisternum absent as a distinct sclerite (fig. 9—Pt. I) 2
   Mesothoracic anepisternum present as a distinct sclerite (fig. 37), ... 5
2. Forewing with vein 3V free at base (2V apparently bifid at base); mesothoracic pre-episternum at its widest much less than one half width of katepisternum (fig. 9—Pt. I); mesomeron with prominent caudal bulge (fig. 9—Pt. I) 3
   Forewing with vein 3V not free at base (2V not bifid at base) (except in *Kallima* *); mesothoracic pre-episternum at its widest at least one half width of katepisternum (except in *Pardopsis*); mesomeron with (rarely) or without (fig. 25) prominent caudal bulge 4
3. Antennae naked; male with a pair of hair pencils at end of abdomen; female protarsus 4-segmented, strongly clubbed (fig. 26—Pt. 1) ..... Danainae
   Antennae scaled; male without a pair of hair pencils at end of abdomen; female protarsus 4- or 5-segmented, not strongly clubbed ..... Ithomiinae
4. Hindwing with cell closed by a well-developed tubular vein (3rd discocellular); tarsal claws usually toothed or asymmetrical, especially in males (normal in *Pardopsis*); gnathos absent or at most vestigial (*Pardopsis*) ..... Acraeinae
   Hindwing cell not closed by tubular vein (3rd discocellular absent or vestigial) (except in *Heliconius, Euides*); tarsal claws simple, symmetrical; gnathos usually well developed, ... Nymphalinae
5. Forewing with veins not swollen; mesothoracic pre-episternum well developed, varying in size, pre-episternal suture usually well developed; hindwing cell often not closed by a tubular vein (see couplet 4) 6
   Forewing usually with at least one vein swollen at base; mesothoracic pre-episternum usually greatly reduced or separated from katepisternum by a very weak pre-episternal suture; hindwing cell always closed by a tubular vein ..... Satyrinae
6. Parapatagia with at least a trace of sclerotization; hindwing cell not closed by a tubular vein ..... Charaxinae

* The base of 3V is present also in *Apaturina* and *Dryas* as a spur which does not anastamose with 2V.

Parapatagia without a trace of sclerotization; hindwing cell sometimes closed by a tubular vein 7

7. Forewing with vein 3V free at base; male with superuncus (fig. 62); female protarsus with small but perfect tarsal claws; hindwing cell closed by a weak tubular vein; humeral cell absent ..... Calinaginae

Forewing with vein 3V not free at base; male without superuncus; female protarsus without claws; hindwing cell open or closed by a tubular vein; species with closed cell also have humeral cell present ..... Morphinae

Danainae

a) Antennae naked; b) interantennal distance variable; c) anterior tentorial arms usually not enlarged anteriorly, no trace of crests (fig. 15); d) parapatagia membranous; e) mesothoracic preepisternum narrow, sometimes almost absent; f) mesothoracic anepisternum not a separate sclerite; g) tegula with distal end relatively blunt (fig. 45); h) mesomeron with a pronounced caudal bulge and sharp caudoventral constriction (fig. 9—Pt. I); i) postcoxal sclerite short (fig. 20, Pt. I); j) arms of gnathos variable, may be absent; k) valvae broad and complex (fig. 36—Pt. I); l) males with hair pencils at the end of the abdomen (fig. 37—Pt. I); m) protarsus of female 4-segmented, clubbed (fig. 26—Pt. I), without well-developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli variable in presence and development; p) forewing without any veins thickened at the bases; q) forewing with base of vein 3V free; r) forewing cell closed by tubular vein; s) hindwing cell closed by tubular vein; t) larvae without bifid tail.

Cosmopolitan but with greatest development in the tropics, especially in the Old World.

Genera examined: *Amauris, Clothilda, Danaus, Euploea, Idea, Ideopsis, Ituna, Lycorea.*

Nothing has been found in the present work which would seem to justify dividing the danaines into tribes. The most obvious variation observed was in the habitus and venation—*Lycorea* and *Ituna* differing from each other and from the rest of the danaines in the facies and the arrangement of the discocellulars of the hindwing. *Euploea* has a lobelike extension of the inner margin of the forewing not found elsewhere in the family. There is some indication that the venation is quite variable within genera or even within species (*e. g.*, most *Lycorea cleobaea* males have much more sharply angled 2nd and 3rd discocellulars than do *L. cleobaea* females).

Considering the structural uniformity of the group and the relatively small number of genera it contains, it would seem best to consider the above-mentioned differences as merely generic.

A great many species of this family are reputed to be distasteful to predators. Butterflies of other groups very often mimic danaines.

Ithomiinae

a) Antennae scaled; b) antennae slightly less than one half the width of the scape apart; c) anterior tentorial arms not enlarged anteriorly, no trace of crests; d) parapatagia membranous; e) mesothoracic pre-episternum completely absent or narrow and set off by distinct pre-episternal suture; f) mesothoracic anepisternum not a separate sclerite; g) tegula with distal end relatively blunt (fig. 44); h) mesomeron with a pronounced caudal bulge and sharp caudoventral constriction (fig. 9—Pt. I); i) postcoxal sclerite long (fig. 53) or short (fig. 20—Pt. I); j) arms of gnathos variable, may be absent; k) valvae variable; l) males without hair pencils at the end of abdomen; m) protarsus of female 4- or 5-segmented, unclubbed, without well-developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at base; q) forewing with base of vein 3V free; r) forewing cell closed by a tubular vein; s) hindwing cell closed by a tubular vein; t) larvae without bifid tail.

Neotropical except for the monobasic genus *Tellervo* which is Papuan.

Genera examined: *Aprotopus, Callithomia, Ceratinia, Dircenna, Hirsutis, Hypoleria, Ithomia, Mechanitis, Melinaea, Napeogenes, Sais, Scada, Tellervo, Thyridia, Tithorea.*

Fox is at present working on the Ithomiinae and has published the first section of his revision (1956). For reasons discussed earlier in this work the ithomiines are considered here to be of subfamilial rank. By nomenclatorially downgrading Fox's system we arrive at two tribes under the Ithomiinae, Tellervini (*Tellervo* only) (male without hair pencil on hindwing, proximal segment of labial palp much more than one half length of second segment), and Ithomiini (all other genera) (male with hair pencil on hindwing, proximal segment of labial palp much less than one half length of second segment). The other tribes recognized by Fox would then become subtribes or genera under the Ithomiini.

Satyrinae

a) Antennae scaled (only on proximal joints of *Pierella* and allies); b) antennae less than one half the width of the scape apart; c) anterior tentorial arms at least somewhat enlarged anteriorly (at least a trace of a crest) (fig. 14); d) parapatagia membranous; e) mesothoracic pre-episternum very reduced in width (fig. 39) or if not very reduced, pre-episternal suture essentially absent; f) mesothoracic anepisternum (fig. 39) a small, but separate sclerite (very small in some genera such as *Erebia, Callerebia*); g) tegulae variable in shape, some with distal end relatively blunt, others with quite pronounced points; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) post-coxal sclerite long (fig. 53) or short (fig. 20—Pt. I); j) arms of gnathos free (fig. 60); k) valvae usually slender (fig. 60) and often dentate; l) males without hair pencils at end of abdomen; m) protarsus of female usually 5-segmented, unclubbed (sometimes extremely reduced as in *Melanargia*); n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing usually with one or more veins thickened at the base; q) forewing with base of vein 3V usually not free (free only in *Pierella, Haetera* and *Callitaera*); r) forewing cell closed by tubular vein; s) hindwing cell closed by tubular vein; t) larvae with bifid tail.

Cosmopolitan, well represented in temperate and arctic regions.

Genera examined: *Anadebis, Antirrhaea, Bia, Callerebia, Callitaera, Coenonympha, Corades, Elymniopsis, Elymnius, Epinephile, Erebia, Euptychia, Gyrocheilus, Haetera, Lethe, Melanargia, Melanitis, Minois, Neope, Oeneis, Pararge, Pierella, Pronophila, Ragadia, Satyrus, Taygetis.*

No attempt is made in this work to divide the Satyrinae into tribes. A number of groups have been previously separated, principally on differences in the venation, for example the condition of base of $Sc + R_1$ and position of 3rd discocellular in hindwing, among others. However, variation in other structures shows some discordance with these venational characters and a thorough generic revision of the subfamily should be completed before final decisions are made concerning its partitioning.

Some of the characters which merit investigation are the form of the genitalia, especially of the gnathos (stubby or absent in *Haetera, Callitaera, Antirrhaea, Pierella, Melanitis,* etc.; well formed in many genera); the shape of the tegulae; the hairiness of the eyes (very hairy in *Lethe* and allies, *Pronophila,* moderately hairy

or naked in many others); development of precoxal suture; development of mesothoracic pre-episternum; and length of postcoxal sclerite (reaching to dorsum of meron in *Bia, Neope, Minois, Elymnius, Haetera, Pierella, Melanitis,* etc., much shorter in *Oeneis, Gyrocheilus, Taygetis, Hipparchia,* etc.).

A detailed study of these as well as many other characters of the satyrines may well show that although there is considerable variation within the subfamily, the genera do not segregate well into tribal groups.

It should be noted that *Bia,* which is placed by some authors (*e. g.,* Clark, 1948) in the "Brassolidae" appears to be a typical satyrine.

The classical character of greatly swollen bases of the wing veins is absent from many satyrine genera (*e. g., Anadebis, Antirrhaea, Lethe, Melanitis, Oeneis*) and is present in many nymphaline genera (*e. g., Bulboneura, Callicore, Cystineura, Pyrrhogyra, Vila*).

Morphinae

a) Antennae scaled or naked; b) antennae less than one half the width of the scape apart; c) anterior tentorial arms at least somewhat enlarged anteriorly (at least a trace of a crest); d) parapatagia membranous; e) mesothoracic pre-episternum well developed, narrow to broad, pre-episternal suture usually well developed; f) mesothoracic anepisternum a relatively large, separate sclerite (fig. 37); g) tegulae variable in shape, some with relatively blunt points distally, others with quite pronounced points; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long (fig. 53); j) arms of gnathos free; k) valvae usually slender and dentate (broad in *Morpho*); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, unclubbed or weakly clubbed without well-developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing veins never thickened at base; q) forewing with base of vein 3V usually not free (free only in some *Taenaris*); r) forewing cell closed by tubular vein; s) hindwing cell open or closed by tubular vein; t) larvae with bifid tail (reduced in *Morpho*).

Indomalayan and neotropical in distribution.

Genera examined: *Amathusia, Brassolis, Caligo, Discophora, Dynastor, Enispe, Eryphanis, Faunis, Morpho, Narope, Opoptera, Opsiphanes, Stichophthalma, Taenaris.*

Considering the present level of knowledge it seems unwise to divide the morphines into tribal groups. The subfamily as a whole seems rather uniform structurally, and most of the characters (venation, foodplant, genitalia, etc.) which have been employed to separate the group into two "families" would doubtless have been considered, at most, subfamilial had the size and popularity of the insects been smaller. Unfortunately the above-mentioned characters show some discordance (*Morpho* differs from most of the others on larval characters, foodplant, genitalia and coloration, etc., while the whole subfamily divides well elsewhere on the basis of several characters of the venation of the hindwing). As in the rest of the butterflies, detailed generic revisions including studies of the immature forms will be needed before a definitive classification can be set up.

Calinaginae

a) antennae scaled; b) antennae less than one half the width of the scape apart; c) anterior tentorial arms with anterior crest (fig. 9); d) parapatagia membranous; e) mesothoracic pre-episternum more than one half width of katepisternum, pre-episternal suture strong dorsally, obsolescent ventrally; f) mesothoracic anepisternum a large, separate sclerite; g) tegula produced distally into a fairly long point (fig. 47); h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long; j) arms of gnathos absent; k) valvae broad, not dentate (fig. 62); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, unclubbed, with well-developed tarsal claws; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at the base; q) forewing with base of vein 3V free; r) forewing cell closed by a weak tubular vein; s) hindwing cell closed by a weak tubular vein; t) larvae unknown.

Represented by a single monobasic genus from the Himalayas.

Genus examined: *Calinaga.*

Charaxinae

a) Antennae scaled; b) antennae usually about one half the width of the scape apart; c) anterior tentorial arms enlarged anteriorly, usually crested (fig. 10); d) parapatagia with at least a trace of sclerotization (fig. 37); e) mesothoracic pre-episternum well developed, usually more than one half width of katepisternum,

pre-episternal suture variable in development; f) mesothoracic anepisternum a large separate sclerite (fig. 37); g) tegula produced distally into a long, relatively fine point; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite long (fig. 53); j) arms of gnathos well developed, free or fused; k) valvae fairly broad, rather simple (fig. 61); l) males without hair pencils at end of abdomen; m) protarsus of female 5-segmented, may be slightly clubbed; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs with aroliar pad and pulvilli present and well developed; p) forewing without one or more veins thickened at the base; q) forewing with base of vein 3V not free; r) forewing cell not closed by a tubular vein; s) hindwing cell not closed by a tubular vein; t) larvae with or without bifid tail.

Tropicopolitan in distribution, sparsely entering temperate regions.

Genera examined: *Anaea, Charaxes, Coenophlebia, Hypna, Prepona.*

No tribal division of the Charaxinae is suggested at this time.

Nymphalinae

a) Antennae scaled (scaling rarely restricted to most basal joints); b) interantennal distance very variable; c) anterior tentorial arms may or may not be enlarged anteriorly; d) parapatagia membranous (except in *Stibochiona*); e) mesothoracic pre-episternum about one half width of katepisternum, often very short and ventral, pre-episternal suture usually well developed; f) mesothoracic anepisternum not a separate sclerite; g) tegulae variable in shape; h) mesomeron without pronounced caudal bulge or sharp caudoventral constriction (fig. 25); i) postcoxal sclerite variable in length; j) gnathos usually present, often complete; k) valvae variable; l) males without hair pencils at the end of abdomen; m) protarsus of female 5-segmented, unclubbed or slightly clubbed; n) pterothoracic legs with tarsal claws simple, symmetrical; o) pterothoracic legs usually with aroliar pad and pulvilli present and well developed; p) forewing sometimes with one or more veins thickened at base; q) forewing with base of vein 3V not free (except in *Kallima, Apaturina* and *Dryas*); r) forewing cell usually not closed by tubular vein; s) hindwing cell not closed by tubular vein; t) larvae without bifid tail.

Cosmopolitan in distribution.

Genera studied: *Ageronia, Agraulis, Apatura, Araschnia, Asterocampa, Boloria, Byblia, Callicore, Catagramma, Catonephele, Catuna, Cethosia, Chlosyne, Cirrochroa, Cupha, Cynthia, Cyrestis, Dichorragia, Didonis, Dione, Doleschallia, Doxocopa, Dryadula, Dryas, Ergolis, Eueides, Euphoedra, Euphydryas, Euptoieta, Euthalia, Gynaecia, Haematera, Heliconius, Historis, Hypolimnus, Kallima, Limenitis, Marpesia, Megistanis, Melitaea, Metamorpha, Morpheis, Neptis, Nessaea, Nymphalis, Panacea, Pandita, Pantoporia, Parthenos, Perisama, Philaethria, Phyciodes, Precis, Pseudergolis, Pyrrhogyra, Salamis, Smyrna, Speyeria, Stibochiona, Temenis, Yoma.*

This large subfamily is more in need of thorough generic work than any other subfamily of the Nymphalidae. This subfamily includes the following subfamilies of Clark (1948): Apaturinae, Marpesiinae, Nymphalinae, Ergolinae, Limenitinae, Argynninae, Heliconiinae. It is possible that some or all of these should be retained as tribes, but additional work is needed before the decisions can be made. Of the above "subfamilies" the Heliconiinae appear to be closest to actual subfamily rank. However, they appear to fall in a continuum between the acraeines and *Argynnis* and allies, with the largest gap coming between the Acraeinae and the heliconians.

Acraeinae

a) Antennae scaled (scales may be sparse); b) antennae about one half the width of the scape apart; c) anterior tentorial arms not prominently enlarged anteriorly, lacking crest (fig. 11); d) parapatagia membranous; e) mesothoracic pre-episternum usually about one half width of katepisternum (except in *Pardopsis* where it is extremely narrow), pre-episternal suture well developed; f) mesothoracic anepisternum not a separate sclerite; g) tegulae very small, blunt distally (fig. 50); h) shape of mesomeron variable; i) postcoxal sclerite short; j) gnathos usually absent (fig. 58), rarely vestigial (*Pardopsis,* fig. 59); k) valvae usually slender, nondentate, simple (except in *Pardopsis,* fig. 59); l) males without hair pencils at end of abdomen; m) female protarsus 5-segmented, unclubbed, without well-developed tarsal claws; n) pterothoracic legs with tarsal claws bifid (toothed) or asymmetrical except in *Pardopsis;* o) pterothoracic legs with aroliar pad and pulvilli reduced (essentially absent) except in *Pardopsis;* p) forewing without one or more veins thickened at the base; q) forewing with base of vein 3V not free; r) forewing cell closed by a tubular vein; s) hindwing cell closed by a tubular vein; t) larvae without bifid tail.

Indomalayan, Ethiopian and neotropical in distribution with the greatest diversity in Africa.

Genera examined: *Acraea, Actinote, Pardopsis, Planema.*

The Acraeinae seem to fall into two tribal groups: Acraeini with a relatively wide mesothoracic pre-episternum, tarsal claws toothed or asymmetrical, reduced aroliar pads and pulvilli, and completely reduced gnathos (*Acraea, Actinote, Planema*); and Pardopsini with a very narrow mesothoracic pre-episternum, tarsal claws simple and symmetrical, well-developed aroliar pads and pulvilli, and a vestigial gnathos (*Pardopsis*).

FAMILY LIBYTHEIDAE

1) Eyes entire; 2) eyes bare; 3) face somewhat to considerably protuberant; 4) laterofacial sutures not contiguous with eye margins; 5) paraocular areas small to large; 6) antennae more than one half width of scape apart; 7) anterior tentorial pits high on face; 8) proboscidial fossa variable in depth; 9) labial palps variable in length, often almost as long as, or as long as the thorax; 10) labial sclerite well sclerotized all around palpal sockets, extended liplike below cervix; 11) anterior tentorial arms enlarged anteriorly, but not downcurved (fig. 13); 12) antennae tricarinate; 13; cervical sclerites not united beneath neck; 14) dorsal plate of pronotum Y-shaped; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella present, but not prominent; 18) lateral plates of pronotum fused dorsally forming a triangular structure; 19) patagia membranous except for a small lateral sclerotic area on each (fig. 26); 20) parapatagia membranous; 21) presternum present; 22) adnotale sagittate (fig. 26); 23) lamella of mesodiscrimen complete to furca; 24) processes of second phragma prominent; 25) precoxal suture present with reduced inflection; 26) pre-episternum of the mesothorax wide (same magnitude as the katepisternum) but pre-episternal suture essentially absent, the presence of the pre-episternum indicated by a notch (fig. 26); 27) mesothoracic anepisternum not a separate sclerite; 28) prescutum vertical or with dorsum anterior to venter (fig. 26); 29) meral suture and lamella absent or not prominent; 30) third phragma consisting of a pair of pointed processes; 31) metatergum essentially overhung by mesotergum (fig. 26); 32) caudal part of metathoracic epimeron intermediate in width; 33; prespiracular bar fully developed; 34) postspiracular bar fully developed, broad (fig. 26); 35) cubitus of forewing appears trifid; 36) 3V of forewing fusing with 2V, not running to inner margin;

37) hindwing with two vannal veins; 38) prothoracic legs atrophied in male, fully developed except for a slight reduction in size in female; 39) protibial epiphyses absent; 40) tarsal claws simple; 41) aroliar pad present, pulvilli present and bifid; 42) pupa without girdle; 43) larva without osmateria.

Cosmopolitan in distribution.

Genera examined: *Libythea, Libytheana.*

In spite of its clearly nymphaloid relationships, this family has been often associated with the riodinines because of the lycaenoid form of the prothoracic legs.

FAMILY LYCAENIDAE

1) Eyes emarginate (fig. 5) (or at least with eye and edge of antennal socket contiguous); 2) eyes bare or hairy; 3) face flat or at most slightly protuberant (fig. 7); 4) laterofacial sutures contiguous or nearly contiguous with eye margins (fig. 5); 5) paraocular areas absent or extremely narrow; 6) antennae close together to very widely separated; 7) anterior tentorial pits usually low on face; 8) proboscidial fossa usually deep; 9) labial palps much shorter than thorax; 10) labial sclerite well sclerotized all around palpal sockets (except in *Styx*), rarely extended liplike below cervix; 11) anterior tentorial arms enlarged and downcurved anteriorly (fig. 17); 12) antennae not carinate; 13) cervical sclerites not united beneath neck; 14) shape of dorsal plate of pronotum variable; 15) spinasternum not laterally produced at spina; 16) profurcal arms simple; 17) intercoxal lamella present, variable in prominence; 18) lateral plates of pronotum fused dorsally to form a V-shaped or triangular structure; 19) patagia membranous (fig. 27); 20) parapatagia membranous; 21) presternum present; 22) adnotale not sagittate; 23) lamella of mesodiscrimen curves downward to base of furca (fig. 42); 24) processes of second phragma prominent or essentially absent; 25) at least a trace of precoxal suture present; 26) pre-episternum usually about same magnitude as katepisternum (fig. 27); 27) mesothoracic anepisternum sometimes present as a separate sclerite; 28) prescutum vertical or nearly vertical; 29) meral suture and lamella absent or not prominent; 30) third phragma variable, but not consisting of simple lobes; 31) metatergum not completely overhung by mesotergum; 32) caudal part of metathoracic epimeron intermediate to thin, not broad; 33) prespiracular bar fully developed; 34) postspiracular bar reduced (may be almost complete) or absent; 35) cubitus of

forewing appears trifid; 36) 3V of forewing when present fusing with 2V, not running to inner margin; 37) hindwing usually with two vannal veins, rarely with only one; 38) prothoracic legs of males moderately to strongly atrophied, almost always clawless, of females slightly reduced in size but with claws; 39) protibial epiphyses absent; 40) tarsal claws simple or weakly bifid; 41) aroliar pad well developed, pulvilli present but not bifid; 42) pupa usually with girdle; 43) larva without osmateria.

Key to the Subfamilies of the Lycaenidae

1. Mesothoracic anepisternum either absent or, if present, not strongly convex; labial sclerite completely sclerotized; male prothoracic tarsi usually neither segmented nor bearing claws, 2

   Mesothoracic anepisternum a prominent, strongly convex, separate sclerite (fig. 38); labial sclerite sclerotized principally behind (strongly) and between (lightly) the palpal sockets; male prothoracic tarsi segmented and bearing a claw each* ..... Styginae

2. Male prothoracic coxae not extending spinelike below articulation of trochanter (slightly extended in *Curetis*); male prothoracic legs more than one half length of pterothoracic legs; hindwing without vein along basal part of costal margin; hindwing with humeral vein usually absent; mesothoracic anepisternum usually not a distinct separate sclerite, Lycaeninae

   Male prothoracic coxae extending spinelike below articulation of trochanter (fig. 57); male prothoracic legs less than one half length of pterothoracic legs; hindwing often with vein along basal part of costal margin; hindwing with humeral vein usually present (when absent vein on costal margin present); mesothoracic anepisternum always a distinct, separate sclerite ..... Riodininae

Styginae

a) Eyes hairy; b) palps very short, approximately same length as head; c) labial sclerite sclerotized principally behind (strongly) and between (lightly) the palpal sockets; d) male prothoracic leg doubtfully functional, less than one half length of pterothoracic legs; e) male prothoracic coxae not extending spinelike below articulation of trochanter; f) male prothoracic tarsus segmented, bearing a tarsal claw (see footnote to key); g) mesothoracic anepisternum a strong convex separate sclerite (fig. 38); h) tegulae small and blunt (fig. 51); i) forewing with two short recurrent veins at

* The single complete male prothoracic leg which it was possible to examine bore only a single tarsal claw. It is quite possible that there was also a second claw which had been broken off.

end of cell; j) hindwing with a humeral vein; k) hindwing without a vein along the costal margin.

Represented by a single monobasic genus from the Peruvian Andes.

Genus examined: *Styx.*

Lycaeninae

a) Eyes hairy or naked; b) palps only rarely as short as head is long; c) labial sclerite completely sclerotized (figs. 3, 4—Pt. I); d) male prothoracic leg functional, more than one half length of pterothoracic legs; e) male prothoracic coxae not extending spinelike below articulation of trochanter (slightly in *Curetis*); f) male prothoracic tarsus usually not segmented rarely bearing tarsal claws; g) mesothoracic anepisternum usually not present as a separated sclerite, when present not prominent or strongly convex; h) tegulae usually rather long (fig. 52); i) forewing rarely with one, never with two recurrent veins at end of cell; j) hindwing usually lacking humeral vein (present in *Pentila, Liptena, Durbania,* etc.); k) hindwing without a vein along the base of the costal margin.

Cosmopolitan in distribution.

Genera examined: *Amblypodia, Atlides, Callictita, Callophrys, Candalides, Cupido, Curetis, Deudoryx, Durbania, Fenesica, Hemiargus Hypochrysops, Hypolyceana, Ialmenus, Incisalia, Lycaena, Lycaenopsis, Lysandra, Mampava, Megalopalpus, Mimacraea, Mitoura, Niphanda, Ogyris, Philiris, Plebejus, Poretia, Pseuderesia, Satyrium, Taraka, Thestor, Telipna, Teriomima, Tharsalia, Thysonotas, Zeltus.*

Riodininae

a) Eyes hairy or naked; b) palps only rarely as short as head is long; c) labial sclerite completely sclerotized (figs. 3, 4—Pt. I); d) male prothoracic leg not functional, less than one half length of pterothoracic legs; e) male prothoracic coxae extend spinelike below articulation of trochanter (fig. 57); f) male prothoracic tarsus not segmented rarely bearing claws; g) mesothoracic anepisternum always present as a separate sclerite, but not prominent or strongly convex; h) tegulae usually rather long (fig. 52); i) forewing rarely with one, never with two recurrent veins at end of cell; j) hindwing with humeral vein usually present; k) hindwing with a vein along the base of the costal margin (always present when humeral vein absent).

Tropicopolitan in distribution, a few nearctic and palearctic. By far most diversely and abundantly represented in the neotropical region.

Genera examined: *Abisara, Anatole, Ancyluris, Anteros, Apodemia, Baeotis, Caria, Diorrhina, Dodona, Echenais, Elaphrotis, Euselasia, Helicopis, Lasaia, Leucochimona, Lymnas, Mesosemia, Metacharis, Nemeobius, Nymphidium, Riodina, Sisime, Stalachtis, Stiboges, Sumachia, Syrmatia, Theope, Thisbe, Zimeros.*

Of all the butterflies the Lycaenidae seem to be most badly in need of detailed work at all levels. Clench (1955) has begun such work with very detailed studies of the male protarsus and other organs. Although the morphological survey and nomenclatorial criteria adopted in the present work have indicated a more conservative treatment than that of Clench, his work seems to be a step in the right direction and the detailed revision which will follow his preliminary work should do much to correct the present situation.

The great mass of the lycaenids seem to divide neatly into the two classical categories "blues" (Lycaenidae *auct.*) and "metal marks" (Riodinidae *auct.*) on the basis of correlated characters in the male prothoracic tarsi and the venation. As discussed earlier these two entities do not seem worthy of more than subfamily rank within the nomenclatorial framework of this work. Time and available material have not permitted an investigation of suprageneric categories within these subfamilies; doubtless many of Clench's groupings will have value there.

A third subfamily, Styginae, is recognized in the present work for the anomalous *Styx infernalis* Staudinger. The lycaenoid character of this insect (which has been placed both in the Pieridae and the "Riodinidae") seems almost beyond question (see diagnoses).* The species is unique but close to the riodinines in the form of the mesothoracic anepisternum; close to the lycaenine *Thestor* in the structure of the male prothoracic leg;† unique in the form of the labial sclerite; unique in the occurrence of two recurrent veins in the cell of the forewing; and perhaps unique in its tendency towards great variation and asymmetry in the anterior veins of the hindwing.

* The male genitalia of *Styx* (fig. 63) are quite lycaenoid.

† Clench (1955) reports fully developed (clawed) prothoracic legs in males of his subfamily Thestorinae. This is based on a detailed examination of *Thestor basuto* Wallengren, and a cursory examination of *T. brachycera* Trimen, and *T. protumnus* Linnaeus. The present author has examined a male of *Thestor ballus* Fabricius and found it to have clawless prothoracic legs.

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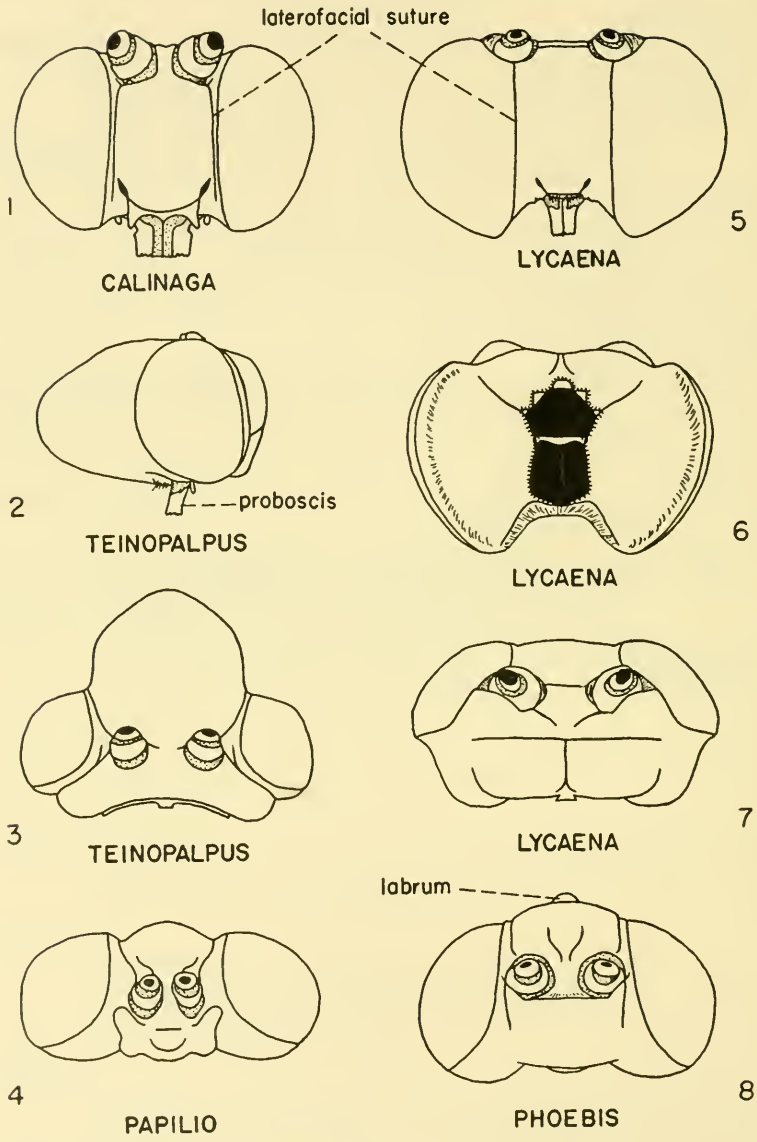
* Not seen.



FIGS. 1-8.* Head. 1. *Calinaga buddha* Moore, front view; 2. *Teinopalpus imperialis* Hope, lateral view; 3. same, dorsal view; 4. *Papilio machaon* Linnaeus, dorsal view; 5. *Lycaena helloides* Boisduval, front view; 6. same, caudal view; 7. same, dorsal view; 8. *Phoebis sennae* Linnaeus, dorsal view.

* Citations of figures followed by "—Pt. I" in the text refer to the illustrations of the monarch butterfly in the first section of this work (Ehrlich, 1958).

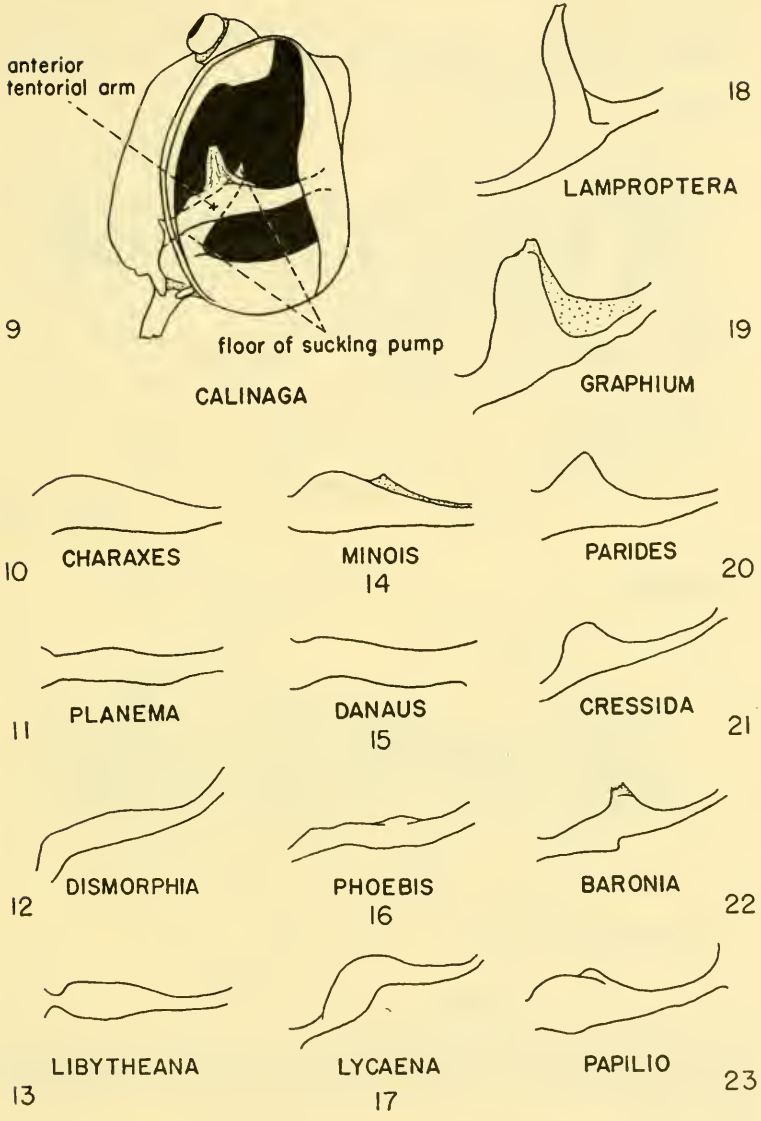
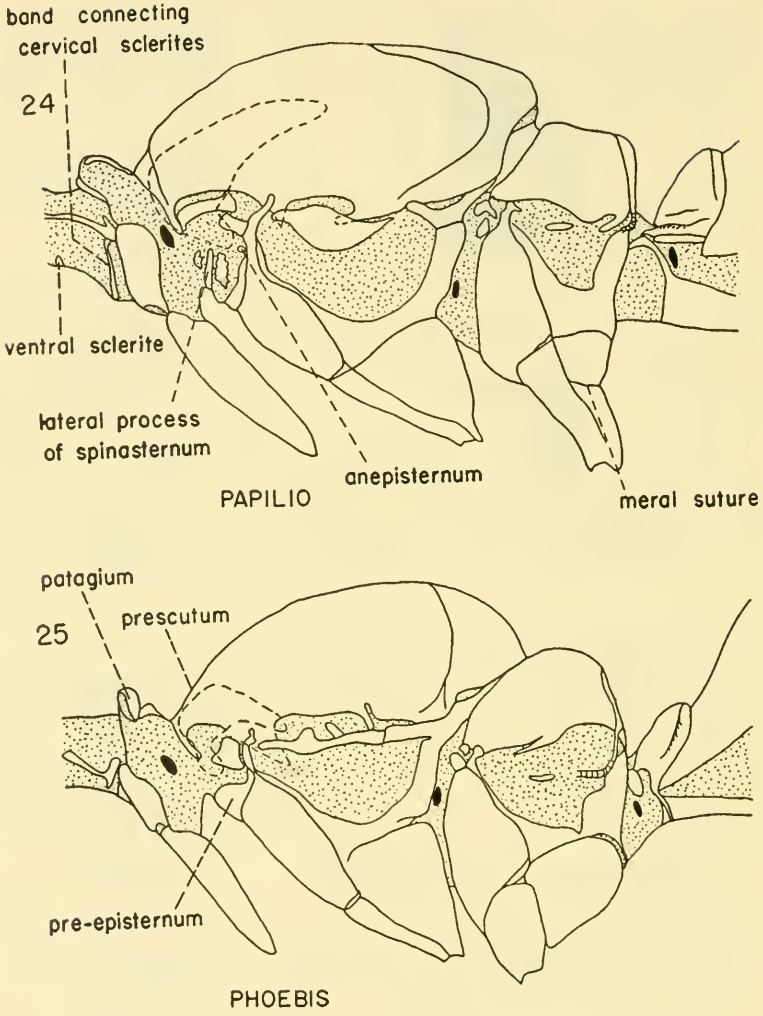
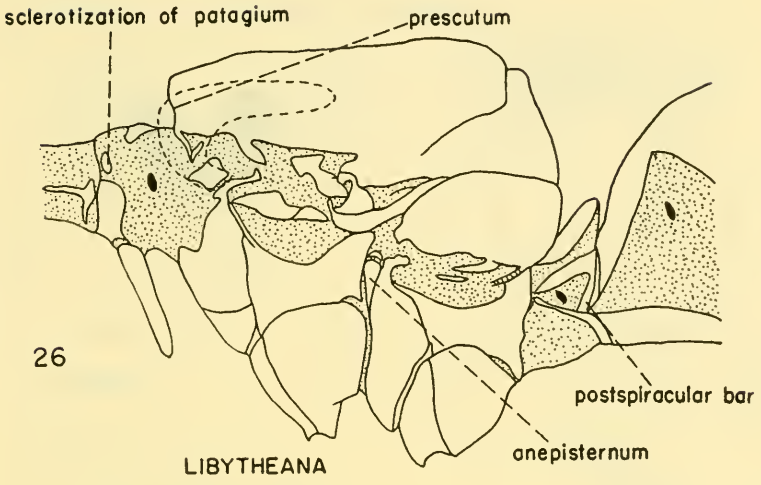
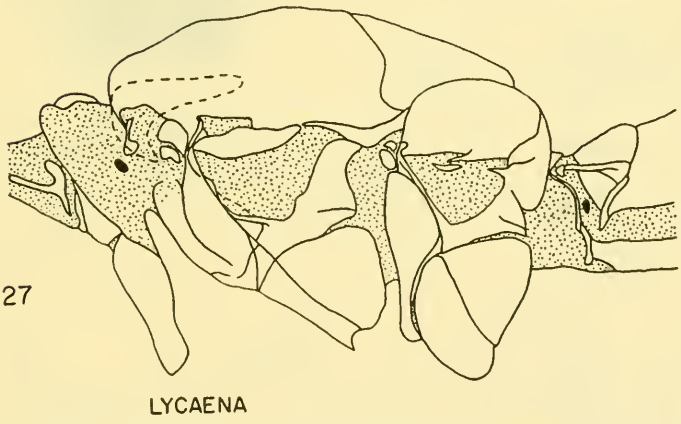


FIG. 9. *Calinaga buddha* Moore, lateral view of head with eye removed to show position of anterior tentorial arm and floor of sucking pump. FIGS. 10-23. Lateral views of anterior tentorial arms, anterior end to left. 10. *Charaxes brutus* Cramer; 11. *Planema aganice* Hewitson; 12. *Dismorphia nemesis* Latreille; 13. *Libytheana bachmanni* Kirtland; 14. *Minois pegala* Fabricius; 15. *Danaus plexippus* Linnaeus; 16. *Phoebis sennae* Linnaeus; 17. *Lycaena helloides* Boisduval; 18. *Lamproptera curius* Fabricius; 19. *Graphium sarpedon* Linnaeus; 20. *Parides polyzelus* Felder; 21. *Cressida cressida* Fabricius; 22. *Baronia brevicornis* Salvin; 23. *Papilio machaon* Linnaeus.

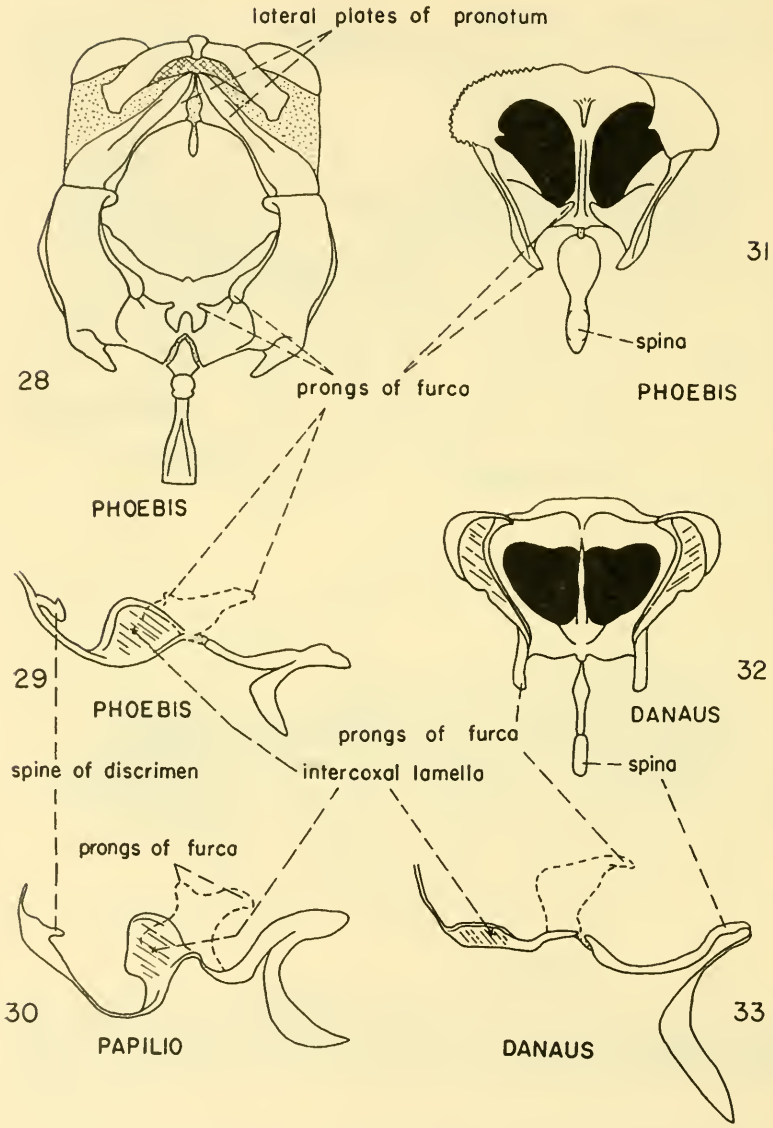


FIGS. 24, 25. Lateral views of cervix, thorax and base of abdomen. Tegulae shown by broken lines. 24. *Papilio machaon* Linnaeus; 25. *Phoebis sennae* Linnaeus.

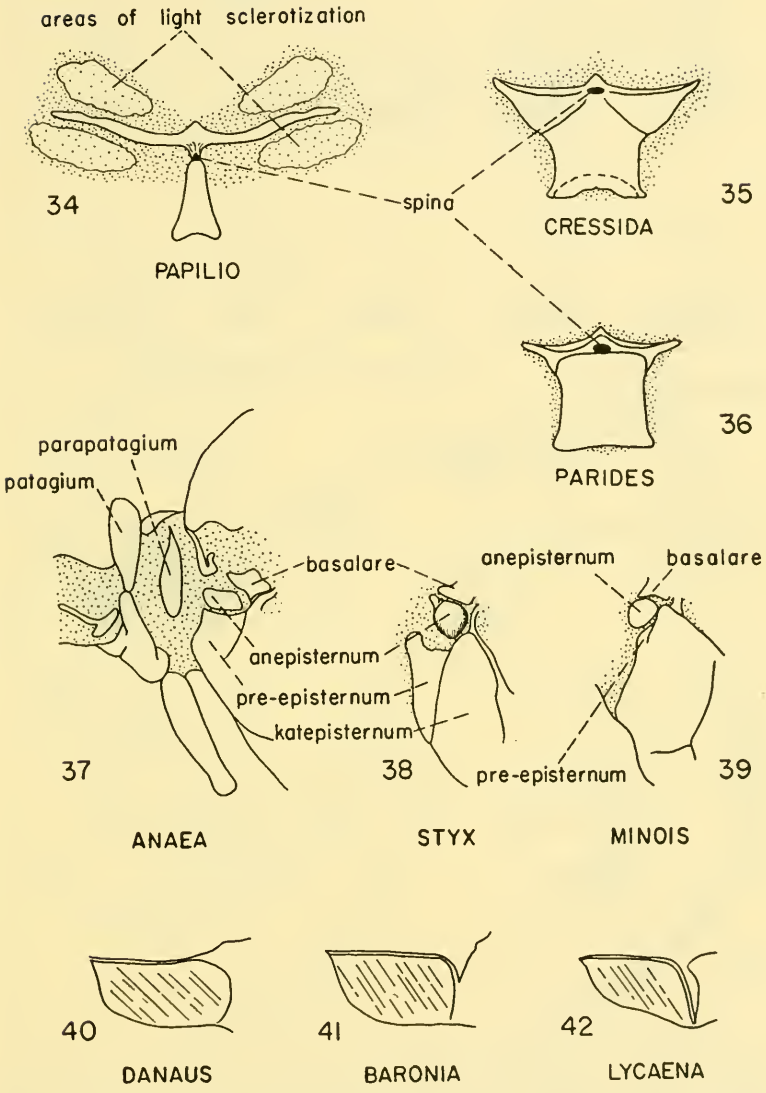




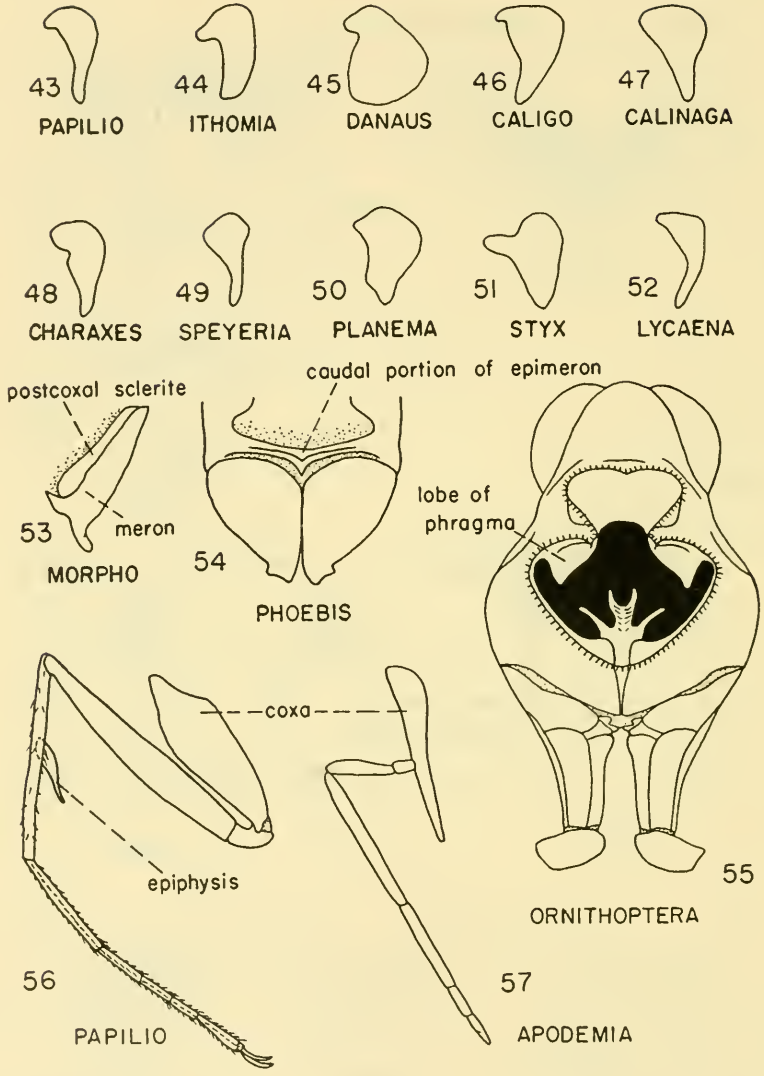
FIGS. 26, 27. Lateral views of cervix, thorax and base of abdomen. Tegulae shown by broken lines. 26. *Libytheana bachmanni* Kirtland; 27. *Lycaena helloides* Boisduval.



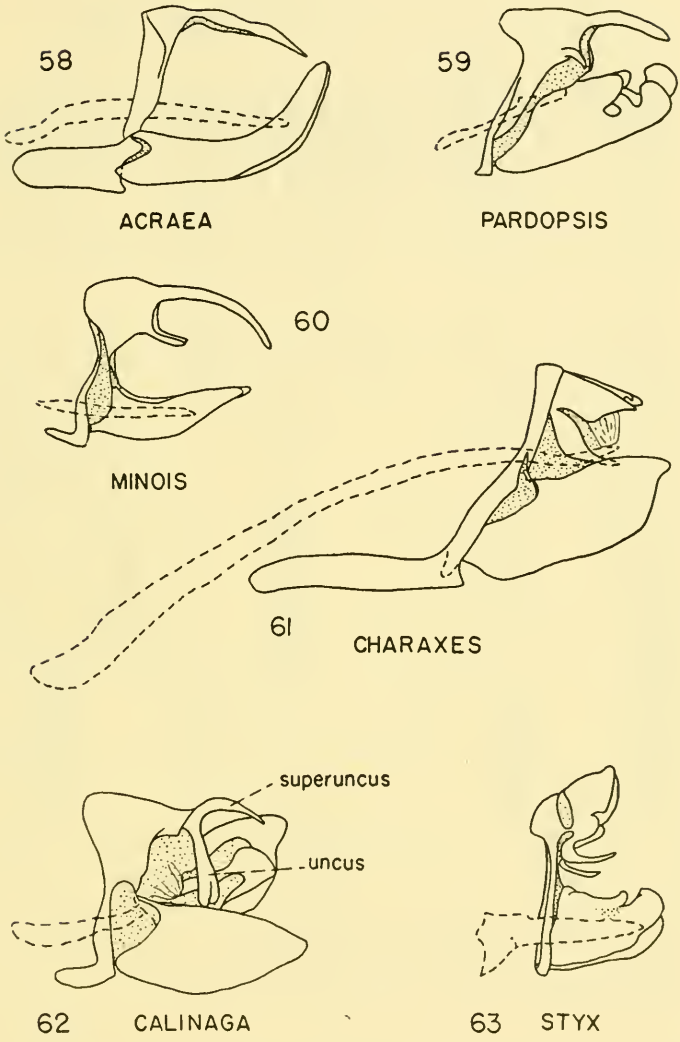
FIGS. 28-33. Prothorax. 28. *Phoebis sennae* Linnaeus, caudal (internal) view; 29. same, lateral view of structures of midline of pleurosternal area, position of furca shown by broken lines; 30. *Papilio machaon* Linnaeus, same view as fig. 29; 31. *Phoebis sennae* Linnaeus, dorsal (internal) view of pleurosternal area, dorsal part of left pleuron removed, spinasternum caudal to spina not shown; 32. *Danaus plexippus* Linnaeus, dorsal (internal) view of pleurosternal area, spinasternum caudal to spina not shown; 33. same, same view as fig. 29.



FIGS. 34-36. Ventral views of spinasterna. 34. *Papilio machaon* Linnaeus; 35. *Cressida cressida* Fabricius; 36. *Parides polyzelus* Felder. 37. *Anaea andria* Scudder, lateral aspect of cervix, prothorax and cephalic portion of mesothorax. FIGS. 38, 39. Lateral views of front portion of mesopleural area. 38. *Styx infernalis* Staudinger; 39. *Minois pegala* Fabricius. FIGS. 40-42. Lateral views of lamella of mesodiscrimen (semidiagrammatic). 40. *Danaus plexippus* Linnaeus; 41. *Baronia brevicornis* Salvin; 42. *Lycaena helloides* Boisduval.



FIGS. 43-52. Outline of tegulae, anterior end upward, ventral side to the left. 43. *Papilio machaon* Linnaeus; 44. *Ithomia cleora* Hewitson; 45. *Danaus plexippus* Linnaeus; 46. *Caligo* sp.; 47. *Calinaga buddha* Moore; 48. *Charaxes brutus* Cramer; 49. *Speyeria cybele* Fabricius; 50. *Planema aganice* Hewitson; 51. *Styx infernalis* Staudinger; 52. *Lycaena helloides* Boisduval. FIG. 53. *Morpho achilles* Linnaeus, caudal view of right mesomeron and postcoxal sclerite. FIG. 54. *Phoebis sennae* Linnaeus, caudal view of metathoracic pleurosternal region. FIG. 55. *Ornithoptera priamus* Linnaeus, caudal view of metathorax (line with short cross lines indicates attachment of intersegmental membrane). FIGS. 56, 57. Prothoracic legs. 56. *Papilio machaon* Linnaeus; 57. *Apodemia nais* Edwards.



FIGS. 58-63. Lateral views of male genitalia, aedaegus shown by broken lines. 58. *Acraea protea* Doubleday and Hewitson; 59. *Pardopsis punctatissima* Boisduval; 60. *Minois pegala* Fabricius; 61. *Charaxes brutus* Cramer; 62. *Calinaga buddha* Moore; 63. *Styx infernalis* Staudinger.

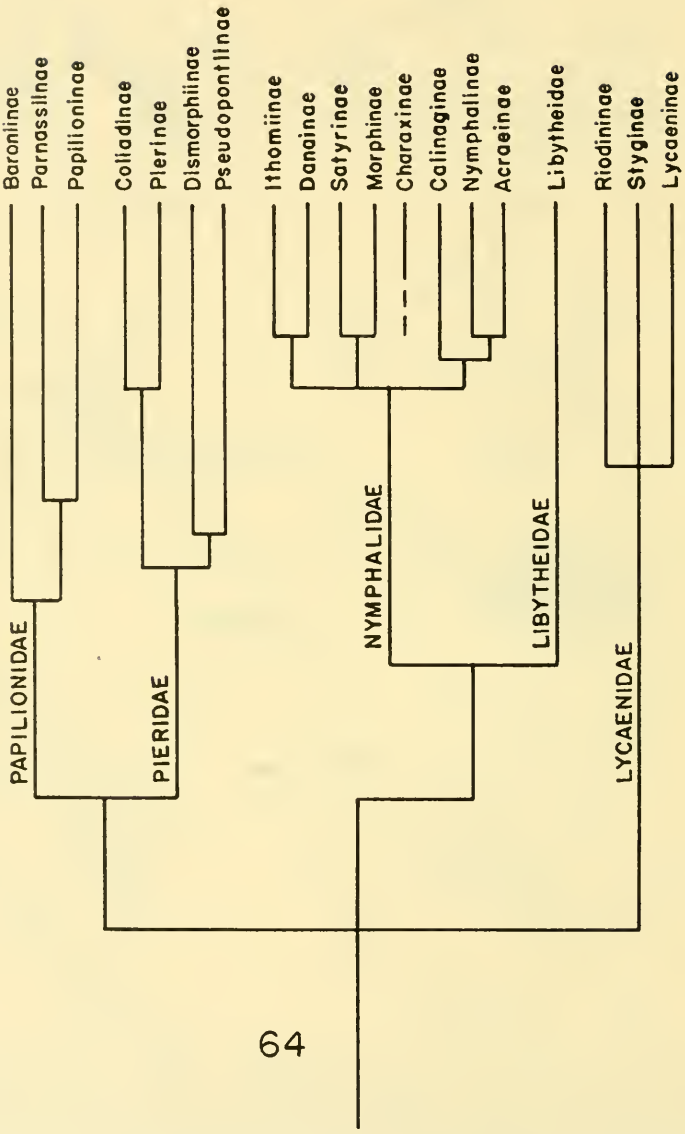


FIG. 64. Relationships of the families and subfamilies of the butterflies.

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The *Tenagogonus-Limnometra* Complex of the Gerridae *

BY

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In 1853, Stål described the genus *Tenagogonus* in Öfvers af K. Vet.-Ak. Förhandl. 10. p. 263 as follows: "Corpus subellipticum Caput subtriangulare, convexiusculum, tuberculis antenniferis parum productis. Antennae corpore longiores, articulis inter se longitudine fere aequalibus, capite nonnihil longioribus; inter articulum 2 et 3 articulus minimus, globosus adest. Rostrum capite ter fere longius, art. 1 capite vix dimidio breviore, 2 hujus dimidia longitudine, 3 capite nonnihil longiore, 4 hoc plus dimidio breviore. Thorax abdomine multo longior, convexus, lateribus subobliquis. Hemelytra et alae desunt. Abdominis segmentum penultimum utrimque ramulum emittens. Pedes posteriores longissimi; tarsi antici breves, crassiusculi, posteriores longiores, graciliores. (spec. 1.)" He did not designate a species but in the introduction to this paper "Nya Genera bland Hemiptera," he states they came from "Cafferlandet."

In 1855, in the same publication vol. 12, p. 45 he described: *"Tenagogonus albovittatus:* supra brunnescens, subtus dilute sordide flavescens, albidosericeus; capitus vittis tribus tuberculisque antenniferis, thoracis linea longitudinali posterius evanescente, vittis 2 anticis abbreviatis, 2 lateralibus aliam dilute flavotestaceum includentibus rostrique art, ultimo nigris; antennis pedibusque fuscotestaceis, his nonnihil dilutioribus. Long. 7-9, lat. 3-3½ millim.—In terra natalensi."

Thus the genus *Tenagogonus* Stål was set up for a species which Stål later described as *Tenagogonus albovittatus.* Fortunately, although the type of this species is in the Museum of Stockholm, Sweden, we have a good series of specimens from West Africa that Dr. O. Lundblad has compared with the type and says is the same species. These are all apterous but we have five specimens from "Gabon," three of which are winged (one male and two females).

* Contribution number 974 from Department of Entomology, University of Kansas. This study was made possible with the aid of a grant from the National Science Foundation.

The distinguishing characters of *Tenagogonus* as set forth by Stål would be: a subelliptical body, a subtriangular head with small antennal tubercles, *antennae longer than the body,* its segments of nearly equal length, each longer than the head and a small intersegment between segments two and three. *Beak nearly three times as long as head,* segment one about half as long as head, segment two very short, three somewhat longer than head and four shorter than half. *Thorax much longer than abdomen. Penultimate abdominal segment with a horn on either side. Hind legs longest.* Front tarsus short, its *second segment longer than the first.*

Then in 1865, Mayr described the genus *Limnometra* in Verhandl. Zool.-bot. Vereins in Wein, Bd. XV, p. 443. This he described as being closest to *Hydrometra* (now *Gerris* Fabricius) with slender antennae as long as body. Hind femora very long, as long as body. Intermediate femora bidentate at apices. Front tarsi with first segment as long or a little longer than the second. Then he described *L. femorata, L. nigripennis, L. pulchra, L. ciliata, L. inermis* and *L. minuta.* Then in Sept. 1865 in Novara-Expedition, Zoologischer Theil, Bd. II, Abth. 1, Hemiptera, p. 174, he gave a key to seven species of *Limnometra* and rewrote the generic description this time saying: Size of Hydrometra. *Antennae* filiform, very slender toward the apex, *as long as the body or sometimes shorter,* basal segment as long as the anterolateral margin of the pronotum. *Beak extending to middle of mesosternum.* Eyes distinctly emarginate on inside. Front margin of pronotum straight, posterior part extending over mesonotum, posterior process triangular. Winged. *Front tarsi* with two claws, *the segments subequal in length. Middle femora apically bidentate, hind femora as long as the body.* The type of the genus *Limnometra* is *L. femorata* Mayr as stated by Dr. Lundblad.

If we compare the descriptions of *Tenagogonus* Stål and *Limnometra* Mayr we find they agree in having long slender antennae, long slender middle and hindlegs and rather long beaks. Possible differences might be that in *Tenagogonus* Stål "Thorax much longer than the abdomen" and "front tarsus short, its second segment longer than the first." While in *Limnometra* Mayr "front tarsi have two segments subequal in length" or "first segment a little longer than the second," "Beak extending to middle of mesosternum" and "Middle femora apically bidentate." The last character is not mentioned in the *Tenagogonus* description nor how far back on the mesosternum the beak extends.

If we examine *T. albovittatus* Stål and *L. femorata* Mayr side by

side they do not appear congeneric. The first is a small species from Africa semielliptical in shape and the male lacks connexival spines but has two conspicuous processes on the ventrolateral margin of the last abdominal segment (7th abdominal segment). Stål mentions these in his generic description as arising from the penultimate abdominal segment which morphologically speaking is not true; moreover, he does not indicate that it is a male character. The abdomen is indeed greatly reduced and much shorter than the thorax, and the enlarged last ventral abdominal segment plus the genital segments in the male are longer than all the preceding abdominal segments. However, the hind legs are shorter than the middle legs, not longer as stated by Stål in his generic description.

In *Limnometra femorata* Mayr we have a large elongate species from the Philippines. The abdomen of the male is elongate, as long or longer than the thorax, with well-developed connexival spines, the last ventral abdominal segment being shorter than the preceding segment and lacking protuberances. Indeed the last abdominal segment plus the genitalia are not as long as the two preceding segments. The beak does not extend to the middle of the mesosternum as stated in Mayr's generic description. The middle femur is apically bidentate, a character we will find of little use. The front tarsal segments are subequal in this species.

In 1901, Champion described *Limnometra opaca* from Panamá and *Limnometra quadrilineata* from Mexico. (Biologia Centrali Americana, Rhynchota vol. II, pp. 180-181.) In 1909, Kirkaldy and Bueno in their Catalogue of American aquatic and semi-aquatic Hemiptera (Proc. Ent. Soc. Washington, vol. X p. 209) gave *Limnometra* Mayr 1865 as a synonym of *Tenagogonus* Stål 1853 and placed *opacus* (Champion) and *quadrilineatus* (Champion) under *Tenagogonus* Stål.

In 1915, Doctor E. Bergroth in a paper entitled "Some Javanese Hemiptera collected by E. Jacobson and Th. H. Mac Gillavry" (Zoologische Mededeelingen uitgegeven vanwege's Rijks Museum van Natuurlijke Historie te Leiden, Deel 1, aflev. 2. pp. 121-123) describes *Tenagogonus pravipes* and states that *Limnometra* Mayr is a synonym of *Tenagogonus* Stål and that *Limnogonus* Stål is not even subgenerically distinct from the above, because "the transitions in the mutual length of the two joints of the fore tarsi and in the apical angles of the last abdominal segment are too numerous."

However, *Limnogonus* Stål is still recognized as a genus and useful as such and his submersion of *Limnometra* Stål is accepted by some and rejected by others. The use of *Tenagogonus* Stål for certain new world gerrids now placed in the genus *Tachygerris*

Drake, was following Kirkaldy and Bueno, 1909. Dr. Poisson, in various papers dealing with African gerrids, follows Bergroth.

In 1925, Dr. W. E. China described *Limnometra gigas* from China, thus bringing again to our attention the genus *Limnometra* Mayr. (Bull. Brooklyn Entomological Society vol. 20, p. 218.) In 1933, Dr. O. Lundblad under *Limnometra* Mayr lists seventeen species and describes *Limnometra brevis.* He states that *Limnometra femorata* Mayr and *Tenagogonus albovittatus* Stål are very dissimilar species and that he is not convinced by Bergroth's opinion that the genera are identical. (Archiv für Hydrobiologie, Suppl. Bd. XII, "Tropische Binnengewässer 4," 388-392, 1933.) Unfortunately, he does not state how these genera may be separated.

Several years ago the senior author became aware of the need for better definition of genera in the Gerridae when called upon to determine species from the East Indies. Dr. Lundblad placed the species *Tenagogonus pravipes* Bergroth, *Gerris kampaspe* Kirkaldy and *L. brevis* Lundblad in the genus *Limnometra* Mayr along with *L. femorata* Mayr and other typical *Limnometra* species and the senior author thought that *Tenagogonus pravipes* Bergroth was correctly named and that *G. kampaspe* Kirkaldy and *L. brevis* Lundblad were congeneric with it.

This has led us into a detailed study of all species we could secure in these two genera. We have re-examined most of the types, made additional descriptive notes, and offer illustrations of them and their structural characteristics. We have studied thirty-seven species from the Old World, nine of them being new. We have placed *Limnometra gigas* China in the new genus *Gigantometra* Hungerford and Matsuda and we are raising *Tenagometrella* Poisson to generic rank to include *T. grandiusculus* Poisson and *T. longicornis* Poisson.

The other thirty-four species have been examined and their position determined on some thirty-five characters. Many of these characters were discarded as generically insignificant when they did not hold for even obviously closely related species. For example, "antennae as long as the body" holds for males of some species but not for their females, while in other very closely related species the male antennae are also shorter than the body.

We have made a chart of the more significant characters and indicated, by number, the species that have these characters. By studying this chart it will be observed that certain species are always found in the line describing a character that is typically *Tenagogonus,* and others are always in a line describing a character that is typically *Limnometra.* In addition there are a few species

that may possess a combination of characters that make them difficult to place. For example in No. 25 *Tenagogonus kuiterti* sp. nov., the male has very small but somewhat variable connexival spines, yet it has the abdominal spiracles in the middle of the segments, has the second front tarsal segment much the longer, the male abdomen is shorter than the mesosternum, and the hind coxae cover the second abdominal segment, all of which relate it to *Tenagogonus*. While all true *Tenagogonus* have the second tarsal segment of the front leg longer than the first there are some *Limnometra*, where the segments are subequal or the second segment a little longer. It is no wonder that Dr. Bergroth gave up trying to separate these genera. However, we do not believe in uniting established genera every time an intermediate species is found. For if we were to follow this practice consistently we would have to unite the families Chrysomelidae and Cerambycidae in Coleoptera, the orders Homoptera and Hemiptera, as some have done and finally unite the Plant and Animal kingdoms! A genus should include a group of closely related species and it is difficult to see close relationship between *T. albovittatus* Stål and *Limnometra femorata* Mayr. It is true that the generic descriptions were both inadequate and inaccurate and we have struggled with this problem for many, many months. We hope that this contribution will be helpful in the identification of species belonging to this complex. We believe it convenient and useful to retain both generic names and redefine them.

NUMBERS AND THE SPECIES FOR WHICH THEY STAND IN THE CHART OF SIGNIFICANT CHARACTERS

1. *albovittatus* Stål
2. *kampaspe* Kirkaldy
3. *divergens* sp. nov.
4. *madagascariensis* Hoberlandt
5. *dubius* Poisson
6. *femorata* Mayr
7. *kirkaldyi* Breddin
8. *fluviorum* (Fabricius)
9. *gigas* (China)**
10. *octopunctata* Hungerford
11. *ciliata* Mayr
12. *cursitans* (Fabricius)
13. *pulchra* Mayr
14. *annulicornis* Breddin
15. *nigripennis* Mayr
16. *inermis* Mayr
17. *vulpina* Breddin *
18. *anadyomene* (Kirkaldy)
19. *palauana* Esaki
20. *brevis* Lundblad
21. *minuta* Mayr
22. *robustus* sp. nov.
23. *pravipes* Bergroth
24. *lipovsky* sp. nov.
25. *kuiterti* sp. nov.
26. *borneensis* sp. nov.
27. *fijiensis* sp. nov.
28. *pravipes bergrothi* subsp. nov.
29. *nudus* Poisson *
30. *hirsutus* Poisson *
31. *lanugineus* Poisson *
32. *zambezinus* Poisson
33. *rossi* sp. nov.
34. *insularis* sp. nov.
35. *kallisto* (Kirkaldy)
36. *longicornis* Poisson **
37. *grandiusculus* Poisson **
38. *euphrosyne* (Kirkaldy)**

* known to us only by descriptions and drawings in the literature.
** removed to a new genus recently or its subgenus is going to be raised to generic rank.

CHART OF SIGNIFICANT CHARACTERS

abdomen ♂ < mesosternum	1,2,3,4,5,20?,22,23?,25,27,28,32,38
abdomen ♂ = mesosternum	18
abdomen ♂ > mesosternum	6,7,8,10,11,12,13,14,15,19,24,26,33,34,35
last ♂ abdominal seg. + gen. = or > than 5 preceding v. abd. segs.	1,2,3,4,5,22,27,28,32,38
last ♂ abdominal seg. + gen. = 4 preceding v. abd. segs.	10,25,33,(24 a wingless ♂)
last ♂ abdominal seg. + gen. < 4 preceding v. abd. segs.	6,7,8,11,12,13,14,15,18,19,24,26,34,35
1st tarsal seg. < 2nd (front leg)	1,2,3,4,5,18,20,21,22,23,25,27,28,32,33,38
1st tarsal seg. = 2nd	10,14
1st tarsal seg. > 2nd	6,8,11,12,13,15,19,24,26,34,35
abd. spiracles in middle	1,2,3,4,5,18,25,27,28,32
abd. spiracles closer to anterior margin	6,7,8,10,11,12,13,14,15,19,24,26,33,34,35
abd. spiracles variable	24,38
♂ without connexival spines	1,2,3,4,5,20,22,23?,27,28,32,(24 in wingless ♂)
♂ with very short connex. spine	24,25,38
♂ with connexival spines or triangular plate	6,7,8,10,11,12,13,14,15,18,19,21,26,33,34,35
♂ with processes on last ventral abd. seg.	1,2,3,4,5
♂ without processes on last abd. seg.	all other species
♂ hind coxae covering 2nd v. abd. seg.	1,2,3,4,5,20?,22,23,25,27,28,32,38
♂ hind coxae *not* covering 2nd v. abd. seg.	6,7,8,10,11,12,13,14,15,18,19,21?,24,26,33,34,35
♂ hind coxae variable	
♂ metasternum > first two abd. segs	1,2,3,4,5,10,20,22,23,25,26,27,32,38
♂ metasternum = first two abd. segs	15,18,19,24
♂ metasternum < first two abd. segs	6,7,8,11,12,13,14,33,34,35
♂ last ventral abd. seg. > preceding seg.	1,2,3,4,5,20,22,23?,25,27,28,32,38
♂ last ventral abd. seg. = preceding seg.	10,18,19?
♂ last ventral abd. seg. < preceding seg.	6,7,8,11,12,13,14,15,24,26,33,34,35

KEY TO TENAGOGONUS-LIMNOMETRA COMPLEX *

1. Male abdomen reduced. Ventral abdominal segments short, last segment plus the genitalia at least as long as preceding four segments, usually longer. Hind coxae of male nearly reaching or surpassing posterior margin of second ventral abdominal segment. Male without typical connexival spines. (Genus *Tenagogonus* Stål) 2

Male abdomen not reduced. Last ventral abdominal segment plus genital segments shorter than preceding four segments. Hind coxae of male rarely extending beyond middle of second ventral abdominal segment. Male with connexivum produced into a triangular flattened plate or spinelike process ... 1a

1a. Pronotum with median longitudinal white line:

Omphalium with transverse channels leading to lateral scent-gland pores, guarded by hairs,
(Genus *Gigantometra* Hungerford and Matsuda)

Omphalium, a circular flat inconspicuous pore, farther from the rear margin of metasternum than in *Limnometra*. No transverse channels.....(Genus *Tenagometrella* Poisson)

Pronotum with median longitudinal black line (Genus *Limnometra* Mayr) 10

2. The last ventral abdominal segment of male with two hornlike protuberances on its caudal edge or venter...*Tenagogonus*.. 3

The last ventral abdominal segment of male without such protuberances 7

3. The protuberances arise on the edge of lateral flaps of the last ventral abdominal segment....*T. madagascariensis* Hoberlandt p. 383

The protuberances not arising as above..... 4

4. The conspicuous protuberances arising just below distal lateral edges of the connexivum in the male..... 5

The protuberances arising farther ventrad..... 6

5. Protuberances upcurved and nearly parallel
T. zambezinus (Poisson) p. 384

Protuberances nearly straight and diverging..*T. divergens*, sp. nov. p. 385

6. The incurved hornlike protuberances arising laterally from the caudal margin of the last ventral abdominal segment,
T. albovittatus Stål p. 382

The short sloping conical protuberances on the ventral surface of the last abdominal segment .....*T. kampaspe* (Kirkaldy) p. 386

7. The male genital capsule (9th segment) with lateral hair tufts . 8

The male genital capsule without lateral hair tufts..... 9

8. The first genital segment of male medianly depressed ventrally with a large V shaped depression in its rear margin,
T. robustus sp. nov. p. 388

The first genital not as above.....*T. brevis* (Lundblad) p. 390

* Omitting Tenagogonus subgen. *Tenagometra* Poisson 1948 in which he places *T. hirsutus* Poisson. *T. lanuginosus* Poisson and *T. nudus* Poisson species which we have not seen. We place in the subgenus *Tenagogonus* the following: *T. albovittatus* Stål, *T. madagascariensis* Hoberlandt, *T. zambezinus* Poisson, *T. divergens* n. sp. and *T. kampaspe* (Kirkaldy).

9. The first genital segment of male with a median longitudinal depressed line on its venter.... *T. pravipes bergrothi* * subsp. nov. p. 393
The first genital segment of male without the depressed line, *T. fijienses* sp. nov. p. 394
10. Connexivum produced into a triangular flattened plate, *Limnometra minuta* Mayr p. 397
Connexivum produced into a spinelike process or an acute projection 11
11. Connexival spines shorter than first genital in the male and in the apterous males may be little more than an acute projection 12
Connexival spines longer..... 14
12. First genital segment of male with its venter normal, rear margin unmodified .....*T. kuiterti* sp. nov. p. 395
First genital segment of male with its venter modified..... 13
13. The first genital segment with a backward pointing protuberance on either side and the venter of the body pale, unspotted, *L. lipovskyi* sp. nov. p. 399
The first genital segment with its rear ventral margin angularly produced on either side. Eight large black spots on the venter .....*L. octopunctatus* Hungerford p. 400
14. Middle coxa with a spinelike projection on the dorsolateral rear margin .....*L. fluviorum* (Fabricius) p. 401
Middle coxa without such projection..... 15
15. Moderately small species. Head width usually under 1.7 mm., even largest males never over 1.76 mm..... 16
Larger than above. Head width usually over 1.8 mm..... 20
16. Front femur as slender as middle femur..... 17
Front femur stouter than middle femur..... 18
17. Antennal segments uniform in color, moderately strong. Second tarsal segment of front leg longer than first. Connexival spines of female very short, not surpassing abdomen, *L. anadyomene* (Kirkaldy) p. 402
Antennal segments three and four and sometimes distal half of second, white, the segments slender and long. First tarsal segment of front leg longer than second. Connexival spines of female long and slender, surpassing abdomen, *L. insularis* sp. nov. p. 404
18. First tarsal segment of front leg longer than second; wing veins dark brown .....*L. palauana* Esaki p. 405
First and second tarsal segments subequal; wing veins not dark brown 19
19. Underside of body pale grayish, including connexivum. The median longitudinal reddish brown line on pronotum, slender and faintly margined by paler bands; marginal dark line faint .....*L. borneensis* sp. nov. p. 407

* This species comes from the Philippines but it seems to fit the description of *T. pravipes* Bergroth from Java and Dr. Bergroth may have overlooked the character on the first genital segment of the male. We are unable to locate the Bergroth types.

Underside of body with brown band on front acetabula and extends back on sides of mesothorax; some brown on the meso-acetabula and underside of connexival segments. The median longitudinal black line on pronotum broad and bordered by broader pale bands, marginal black band prominent,
L. rossi sp. nov. p. 408

20. Antennae, middle and hind femora uniform in color, the latter not paler near tip. Middle femur of male with conspicuous long cilia 21
Antennae, middle and hind femora not uniform in color, the latter at least slightly to conspicuously paler near tip. Middle femur of male may have cilia (but not as long as the diameter of the femur) 22

21. Middle femur with a short black line near base dorsally. Rear ventral margin of first genital segment of male produced laterally (see pl. 14, fig. 22d.) ..... *L. ciliata* Mayr p. 409
Middle femur without the black line. Rear margin of first genital segment of male with faint production laterally,
L. cursitans (Fabricius) p. 413

22. Middle femur of male with two rows of pegs and a large curved spine near distal end ..... *L. femorata* Mayr p. 413
Middle femur of male may have two rows of pegs but without the large curved spine near distal end 23

23. Middle femur of male without definite fringe of long cilia. Hemelytra usually chocolate brown with costal margin yellow or orange. Mesosternum not ciliated. Second and third antennal segments usually ringed with white and last segment white ..... *L. nigripennis* Mayr p. 415
Middle femur of male with definite fringe of cilia. Hemelytra not as above. Mesosternum of males usually ciliated. Antennae not as above 24

24. Both middle and hind femora of male with definite fringe of cilia ..... *L. pulchra* Mayr p. 418
Only middle femora of male with definite fringe of cilia 25

25. Second antennal segment annulated, shorter or subequal to width of head across eyes. First and second tarsal segments of front leg subequal ..... *L. annulicornis* (Breddin)* p. 420
Second antennal segment not annulated, usually longer than width of head across eyes. First tarsal segment of front leg plainly longer than second ..... *L. kallisto* (Kirkaldy) p. 422

* *L. vulpina* Breddin—The type female from "N. [Matinag Kitte, Sudsaite, 800-1200 m (Sar.)]" we cannot locate. Since Dr. Breddin identified specimens of *L. pulchra* Mayr as his *L. annulicornis* and the females of *L. pulchra* have shorter connexival spines he probably compared his female *L. vulpina* with a female of *L. pulchra* Mayr and said its connexival spines were longer than *L. annulicornis* when his *L. vulpina* was really a female of his *L. annulicornis*.

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SYSTEMATIC TREATMENT

The genera *Tenagogonus* Stål and *Limnometra* Mayr have in common: Rather long antennae, slender beaks with third segment reaching onto the mesosternum, long middle and hind legs and venation of hemelytra.

The Genus *Tenagogonus* Stål

1853 Stål, C. Öf Vet. Akad. Förh. 10 pp. 263-264. (Described from "Cafferlandet" for one species unnamed.)
1855 Stål, C. Öf Vet. Akad. Förh. 12 (1): 45. (Described *Tenagogonus albovittatus*, which is the type of the genus.)
1865 Stål, C. Hemiptera Africana 3: 168-169. (Assigns to *Tenagogonus* Stål the species *T. fluviorum* (Fabricius) and *T. swakopensis* Stål but does not mention his *T. albovittatus*.)
1909 Kirkaldy, G. W. and Torre Bueno, J. R. de la. Proc. Ent. Soc. Washington, 10: 209. (Give *Limnometra* Mayr as synonym of *Tenagogonus* Stål.)
1915 Bergroth, E. Zool. Med. Rijks Mus. Nat. Hist. Leiden, 1 (2): 121-123. (Gives *Limnometra* Mayr as synonym.)
1916 Bergroth, E. Proc. Nat. Mus. 51, 2150: 237.
1933 Lundblad, O. Archiv für Hydrobiologie 1933 Suppl. 12, "Tropische Binnengewässer 4," pp. 388-392.
1948 Poisson, R. Mem. Inst. Sci. Madagascar, ser. A, 1 (2): 94-95. (Proposes subgenera of *Tenagogonus*.)

Rather small gerrids, with moderately long antennae, middle and hind legs. Male with last ventral abdominal segment plus genital segments equal to or greater than preceding four ventral segments, usually as long as or longer than preceding five ventral abdominal segments. Front leg with first tarsal segment shorter than second. Abdominal spiracles in middle of segments. Male without or with very short connexival spines. Males with hind coxae covering second ventral abdominal segment. Male metasternum longer than first two ventral abdominal segments. Male last ventral abdominal segment greater than preceding segments. In *Tenagogonus* the males are usually smaller than the females.

Tenagogonus albovittatus Stål

(Pl. 1, fig. 1; Pl. 7, fig. 1)

1853 *Tenagogonus*. Stål, C. Öf Vet. Acad. Förh., 10: 263-264. (New genus described from "Cafferlandet" for one species unnamed.)
1855 *Tenagogonus albovittatus* Stål, C. Öf Vet. Akad. Förh., 12 (1): 45. (Described from Natal.)
1916 *Tenagogonus albovittatus* Bergroth, E. Proc. Nat. Mus. 51 (2150): 237.
1940 *Tenagogonus albovittatus* Poisson, R. *nec* Stål. Bull. Mus. Roy. Hist. Nat. Belg. 16 (40): 5-7 (= *T. zambezinus* Poisson.)
1941 *Tenagogonus albovittatus* Poisson, R. *nec* Stål. Rev. Franc. Ent. 8 (12): 77.
1948 *Tenagogonus albovittatus* Poisson, R. *nec* Stål Mem. Inst. Sci. Madagascar 1: 95.
1952 *Tenagogonus albovittatus* Poisson, R. *nec* Stål Res. Nat. Integrale du Mt. Nimba. 13: 282.
1954 *Tenagogonus* (s. g. *Tenagogonus*) *albovittatus* Poisson, R. Institut des Parcs Nationaux du Congo Belge. Exploration du Parc Nat. de l'Upemba 31, 3-4.

Our specimens are represented by one winged male and two winged females, one wingless male and one wingless female from Gabon, French Equatorial Africa; nine wingless females from Sangmelina, West Africa.

Size: 6.7—7.4 mm. long; width across mesoacetabula 2.4—2.6 mm. in wingless male. 7.3—7.6 mm. long; width 2.85—3.1 mm. in wingless female. 9.2 mm. long in winged male and 7.4 mm. long in winged female.

Color: Dark reddish brown in ground color. Head above with median black longitudinal stripe continuous with black clypeus and a pair of lateral black stripes. Rostrum yellowish brown except for its last segment which is black. Antennae dark reddish brown. Pronotum with median black longitudinal stripe bordered by yellowish area and wide black spot on either side of its median longitudinal stripe in anterior lobe, lateral and posterior margins also black as shown in figure. Mesonotum on either side of pronotum with a broad white area. Body beneath yellowish.

Structural characteristics: Proportional length of antennal segments: 1st: 2nd: 3rd: and 4th:: 52: 55: 60: 65 in one wingless male, and 50: 45: 47: 63 (curved) in one wingless female. Front femur about as thick as middle femur and slightly curved in both sexes.

The relative length of leg segments in a wingless male:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	76	67	10	12
Middle leg	183	150	46	12
Hind leg	175	80	17	9

Hind legs much longer than length of body. Structures of seventh and first genital segments are quite characteristic in male as shown in the figures. Winged form: shape of pronotum and hemelytra as shown in the figures. Sc_2 vein joins with R + M at the point of forking of the latter.

Location of types: Naturhistoriska Riksmuseum, Stockholm.

Comparative notes: Broad white band on the mesonotum and peculiar structure of the seventh ventral abdominal and first genital segments in the male readily separate this species from the other related species within the genus *Tenagogonus*. *Tenagogonus dubius* Poisson, according to personal letter from Dr. Poisson, is closely related to *T. albovittatus*, if not synonymous. The specimens from Congo Belge identified as *T. dubius* by Dr. Poisson shows actually very little difference from the specimens from Cameroons, West Africa, identified as *T. albovittatus* Stål by Dr. Lundblad. Whether these two species are the same species or not awaits further investigation.

Tenagogonus madagascariensis Hoberlandt

(Pl. 1, fig. 3; Pl. 7, fig. 3)

1947 *Tenagogonus madagascariensis* Hoberlandt, Acta Ent. Mus. Nat. Prag. 25: 105-112. 3 plates.
1948 *Tenagogonus madagascariensis* Poisson, R. Mem. Inst. Sci. Madagascar, 1: 89. Figs. 5, 6, 7.
1948 *Tenagogenus* (s. g. *Tenagogonella*) *madagascariensis* Poisson, Mem. Inst. Sci. Madagascar, 1: 93-94.

Size: 7.3 mm. long; width across mesoacetabulae 2.2 mm. in a wingless male paratype. 8.3-8.9 mm. long; width across mesoacetabula 2.95 - 3.35 mm. in wingless female paratypes.

Color: Yellowish brown to fuscous in general color. Head with usual three black longitudinal stripes on upper surface. Pronotum with median longitudinal black stripe and broad lateral stripes, posterior lobe occasionally nearly black, subject to individual variation in degree of black pigmentation. Mesonotum yellow on median longitudinal axis, sides fuscous; mesopleural region with broad longitudinal fuscous band. Metanotum and basal abdominal tergites darker, sometimes entirely black. Body beneath yellow, last rostral segment black.

Structural characteristics: Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 52: 52: 62: 83 in one wingless paratype male; 50: 40: 45: 60 (? curved) in one wingless paratype female.

The relative length of leg segments in one wingless male:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	72	60	7	10
Middle leg	163	130	53	12
Hind leg	155	73	18	11

Middle legs longer than length of body. Front femur a little thicker than base of middle femur; middle femur much thicker than hind femur. Pronotum prolonged to about middle of mesonotum. No winged form is known.

Location of types: National Museum of Praha. Three wingless males and three wingless female paratype specimens are at University of Kansas.

Comparative notes: This species can readily be distinguished from the rest of the species of *Tenagogonus s. str.* by the short pronotum. The seventh abdominal and first genital segments are conspicuously modified ventrally, as in other species of *Tenagogonus s. str.*, but they can be recognized from the accompanying figures.

Data on distribution: Madagascar: "Vohemar, Ambomja" (type series, Hoberlandt); "Mahilaka (Sambirano); forêt des Roussettes (Montagne d'Ambre)" (Poisson); "(Tananarive)" (New record). 28 wingless males and 56 wingless females from Tananarive, Madagascar are preserved in the Francis Huntington Snow Entomological Museum, University of Kansas.

Tenagogonus zambezinus (Poisson)

(Pl. 1, fig. 2; Pl. 7, fig. 2)

1934 *Gerris* (*Limnoporus*) *zambezinus* Poisson, R. Bull. Soc. Zool. France, 59 (1): 92-93.
1940 *Tenagogonus albovittatus* (? *Gerris [Limnoporus] zambezinus* Poisson) Poisson, R. Bull. Mus. roy. Hist. nat. Belg., 16 (40): 5-7.
1941 *Tenagogonus albovittatus* Poisson, R. Rev. Franc. Ent., 8 (2): 77.
1948 *Tenagogonus albovittatus* Poisson, R. Mem. Inst. Sci. Madagascar, 1: 95.
1952 *Tenagogonus albovittatus* Poisson, R. Res. Nat. Integrale du Mt. Nimba, 13: 282.

Dr. W. E. China kindly loaned us one identified wingless male and one female specimen. The following description is based on them.

Size: 8.5 mm. long; width across mesoacetabula 2.77 mm. in one wingless male. 9.9 mm. long and 3.75 mm. wide in one wingless female.

Color: Pale reddish brown in ground color, with black markings on dorsal surface; black pigmented area densely clothed with short

adpressed grayish hairs. Head with usual three black stripes. Pronotum with median black longitudinal stripe and lateral narrow marginal black stripes evanescent apically, a pair of broad short black bands on either side of middle of anterior lobe. Mesopleural region with three black stripes which are confluent anteriorly and posteriorly, each abdominal tergite from second segment on with a pair of black markings. Connexivum darker laterally or with a continuous median longitudinal black stripe. Rostrum yellow except the last segment black. Body beneath pale yellow.

Structural characteristics: Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 24: 23: 27: ? in wingless male and 26: 20: ?: ? in wingless female.

The relative length of leg segments in one wingless male is as follows:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	77	63	10	12
Middle leg	172	147	40	?
Hind leg	165	90	18	10

Seventh segment in male with ventrolateral processes long and they arise more dorsally than in the preceding species. Eighth segment without conspicuous modification ventrally in male.

Location of types: Musée Royal d'Histoire Naturelle de Belgique.

Comparative note: Relatively large. The shape and location of the process on ventrolateral margin of seventh segment in male and the simple posterior margin of eighth ventral abdominal segment readily separate this species from the rest of *Tenagogonus*.

Data on distribution: Mzingaze, environ de Vila Pery, Bas Sandgazé; Calamo (Poisson 1934, 1940).

The specimens we examined bear the following labels: "S. Africa, G. E. Hutchinson call. B. M. 1928-395." "S. Rhodesia" 1 apterous male (British Mus.). "Zululand, Nagapa Res. Lab. 23-IV-1922 H. H. Curson" 1 apterous female (British Mus.).

Tenagogonus divergens n. sp.

(Pl. 1, fig. 4; Pl. 7, fig. 5)

Size: Apterous male holotype 7.56 mm. long; width across the mesoacetabula 2.646 mm.; width across the head 1.47 mm.

Color: Light brown. Head with two reddish brown spots above the clypeus and a curved line near each eye; pronotum with median longitudinal reddish brown line and another near its margin; dark brown band on propleuron behind the eye and continued as two

bands to mesopleuron, the upper one ending behind mesoacetabulum; two short bands on mesoacetabulum; two longer ones on metaacetabulum; under side of connexivum dark; remainder of venter pale except for short black spot at anterior end of mesoacetabular cleft.

Structural characteristics: Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 96: 86: 126: 140. Total length of antenna 9.4 mm. Beak slender. Front leg segments: femur: tibia: 1st tarsal: 2nd tarsal:: 150: 127: 16: 26. Middle femur 390 spaces or 8.19 mm. long, remaining segments and hind legs missing. Abdominal segments rather short, the first two ventral abdominal segments together shorter than metasternum. Hind coxa surpassing rear margin of second ventral abdominal segment. Last ventral abdominal segment of male slightly shorter than the two preceding segments. Conspicuous diverging protuberances arising from the surface of the last ventral abdominal segment just beneath connexivum.

Location of Type: Described from a specimen bearing the label "Brook near Bawomataluwo, Sumatra, 9-12-31. v. d. Meer Mohr." (K. U. col.)

Comparative notes: This species has the protuberances of the last ventral abdominal segment of the male arising just beneath the connexivum instead of farther ventral as in *T. albovittatus* Stål. In this regard it is more like T. *zambezinus* Poisson.

Tenagogonus kampaspe (Kirkaldy)

(Pl. 1, fig. 5; Pl. 7, fig. 4)

1900 *Gerris Kampaspe* Kirkaldy, G. W. Ann. Mus. Civ. Stor. Nat. Genova, ser. 2, 20: 804.
1933 *Limnometra kampaspe* Lundblad, O. Archiv für Hydrobiologie Suppl. 12, "Tropische Binnengewässer 4," p. 371 (quotes New Guinea).

The original description: "*Gerris kampaspe* sp. n. Belongs to subg. *Limnometra* Mayr. Size and general structure of *minuta* Mayr, but readily distinguished by its much greater breadth. Fulvo-cinereous; a diamond-shaped mark on the head, a median longitudinal line on the pronotum, and legs blackish brown. Venter pale cinereous. Elytra dark fulvo-cinereous with blackish nervures. Length 5½ - 7½ mm. New Guinea: Kelesi (Loria), Rigo (Loria)."

Fortunately, the type series, two males and two females, are in the Kirkaldy collection at the University of Kansas Entomological Museum, otherwise we would never have been able to recognize

it. No specimens are now entire but the following notes and the illustrations should enable one to identify the species.

Size: Winged male: 5.33 mm. long; width across humeri 1.43 mm.; width across mesoacetabula 1.7 mm.; width across head 1.16 mm.; wingless male: 4.2 mm. long; width across mesoacetabula 1.64 mm.; width across head 1.09 mm. Wingless female: 6.3 mm. long; width across mesoacetabula 1.64 mm.; width across head 1.43 mm.

Color: General color rather light yellowish-brown; the reddish black figures as shown in the illustration; dark brown to black band on propleuron behind the eyes; the two bands on mesopleuron more or less fused; a brown spot on lateral margin of mesosternum may be present. Venter pale.

Structural characteristics: One winged male with two antennal segments: 1st: 2nd:: 57: 50. One wingless female with three antennal segments: 1st: 2nd: 3rd:: 80: 66: 76. One specimen, a male with a beak reaching one third the distance on mesosternum. Front femur of male considerably stouter than middle femur and strongly curved, other legs incomplete.

Relative length of leg segments of a winged male:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	85	78	9	11
Middle leg	190	160	?	?
Hind leg	190	100	21	12

Middle femur not as long as body in either sex. Connexivum rather broad; no connexival spines. Dorsal abdominal segments of male short; last one as long as two preceding. Hind coxa of male reaching penultimate abdominal segment; of female reaching rear margin of second abdominal segment. Abdominal venter of male a little more than half as long as mesosternum, its last abdominal segment plus genital segments longer than the rest of abdomen; the venter of last abdominal segment of male with caudally directed lateral protuberances.

Winged form: Shape of pronotum and venation of hemelytra as shown in illustration.

Location of types: Described from two males, one winged, and two wingless females labeled as follows:

The winged male: "N. Guinca Mer. Kelesi, Nov. Dic. 1890. L. Loria." "*Gerris Kampaspe* Kirk. Type ♂." Wingless male: "N. Guinea Mer. Rigo, Luglio 1889. L. Loria." One wingless female: "N. Guinea. Dilo, Loria VI, VII 90." One wingless female: "N.

Guinea Mer. Rigo, L. Luglio 1889." This one bearing the same label as the type should be considered the allotype. These are in the Kirkaldy collection of The University of Kansas Snow Entomological Museum.

Comparative notes: This species is related to the *T. albovittatus* Stål group.

Data on distribution: Known so far only from these types from New Guinea.

Tenagogonus robustus sp. nov.

(Pl. 1, fig. 6; Pl. 8, fig. 9; Pl. 16, fig. 30; text fig. 1)

Size: Apterous male: 7.56 mm. long; width across the mesoacetabula 3.15 mm.; width across the head 1.64 mm. Apterous female: 7.35 mm. long; width across the mesoacetabula 3.15 mm.; width across the head 1.57 mm.

Color: Yellowish to reddish brown. Head with a short dark median band on its base that splits into two diverging bands that suddenly converge to unite before the base of clypeus, an undulate band near each eye; pronotum with usual median longitudinal line; lateral dark lines near the margin that are broad on the anterior lobe. Abdominal dorsum more or less mottled with darker brown; black band on propleuron behind the eyes and continued as two broad bands separated by a narrow pale line; the upper band broader and continuing onto metaacetabula, the lower one turning down at its end but not connecting with the dark band on mesoacetabula. Venter nearly white; underside of connexivum embrowned.

Structural characteristics: Proportional length of the antennal segments of male: 1st: 2nd: 3rd: 4th:: 100: 84: 107: 116. Total length of antenna 8.55 mm. Beak moderately slender, covering less than one third of mesosternum. Front femur slightly, if any shorter, than middle femur.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	157	137	17	30
Middle leg	385	270	114	30
Hind leg	330	200	40	35

Posterior lobe of pronotum in apterous forms rather narrow and exposing mesonotum around its tip. Connexivum rather broad, no connexival spines. Dorsal abdominal segments of male fairly short, last one as long as the two preceding. Hind coxae of male reaching rear margin of third ventral abdominal segment; of female sur-

passing the middle of second ventral abdominal segment. Last ventral abdominal segment of female as long as the two preceding segments. In the male the last ventral abdominal segment as long as the two preceding segments and together with genital segments longer than the rest of abdomen. First genital segment of male medially depressed ventrally, with a large V-shaped notch on its rear margin. Male genital capsule (9th segment) with lateral hair tufts.

Location of types: Described from 3 males 3 females from Sumba, five of them bear the label "Prai Jawang, O. Sumba, Rende Wai, 14. 6. 1949, Dr. Bühler, Dr. Stutter." and one with the label "Pogobina 17. 9. 1949, Dr. Bühler, Dr. Stutter." These and one bearing the label "Ost-Java Lavang 1.500′ Leg. M. E. Walsh 136" were sent to us for determination by the Museum at Basel, Switzerland. The holotype, allotype and two paratypes will be found there and two paratypes in the University of Kansas collection. Through kindness of Mr. A. M. R. Wegner of the Zoological Museum at Bogor, Indonesia, we have recently been loaned an apterous male and female, two winged males and one winged female bearing the label "Coll. F. C. Drescher, Java, Preanger N. O. I. Bandoeng, 750 m. 1937." These were labelled *Limnometra brevis* Lundblad but not by Lundblad, they are actually our *T. robustus* and are made paratypes. Four of these have been returned to the Museum at Bogor.

Comparative notes: This species is most closely related to *Tenagogonus brevis* (Lundblad), from which it is readily distinguished by the shape of the first genital segment of the male, and by its parameres which are quadrate in shape not pointed as in *T. brevis* (Lundblad).

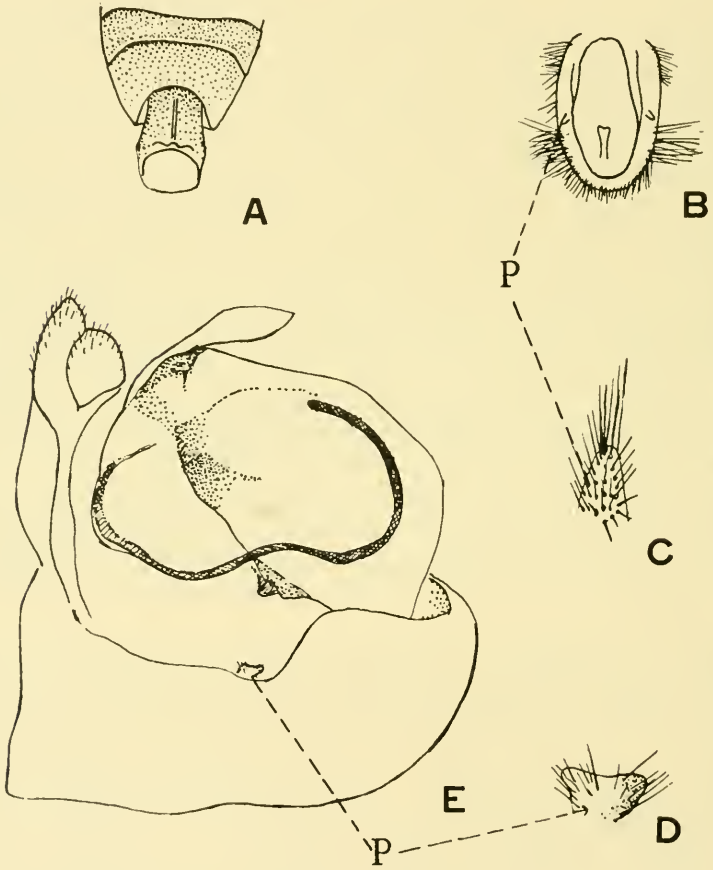
Data on distribution: Besides the Sumba and Ost-Java records above we have two females that bear the label "Mt. Apo, Mindanao, Philippine Islds. C. F. Clagg, Baroring Riv. 7.000 ft. Nov. 8." These came to us for determination from the Museum of Comparative Zoology at Harvard College. In size, shape and color pattern they are almost identical with this O. sumba species. However, since they came from the Philippines and have the posterior lobe of the pronotum somewhat broadened at the humeri and have moderately long and spine like projections on the connexivum that are entirely lacking in the Sumba species we believe they represent a good subspecies and give them the name *Tenagogonus robustus claggi* n. subsp. Males, when they are found, may indicate a good species (see pl. 2, fig. 7; pl. 8, fig. 10). One specimen is in M. C. Z. and the other is in the Snow Entomological Collection, University of Kansas.

Tenagogonus brevis (Lundblad)

(Pl. 2, fig. 8; Pl. 2, fig. 6)

1933 *Limnometra brevis* Lundblad, Archiv für Hydrobiologie 1933, Suppl. 12. Tropische Binnengewässer 4, pp. 388-392, Taf. 10, fig. 123.

Thanks to Doctor Lundblad we have seen the winged allotype of this species and have had it redrawn to conform in magnification with the other species reported in this paper and also have had



TEXT FIGURE 1.

(A) Abdominal venter and first genital segment of male of *Limnometra brevis* as drawn by Lundblad in his figure 123 D on page 391. (B) Genital capsule of *L. brevis* Lundblad as shown in above text figure 123 E showing location of paramere or "genital griffel" at p. (C) Paramere of the above enlarged. (D) Paramere of *Tenagogonus robustus* n. sp., enlarged. (E) Genital capsule of *T. robustus* from left side showing paramere at p.

his drawing of the apterous female enlarged. His description and illustrations are splendid and adequate.

In the allotype the last antennal segment appears nearly white but the middle and hind femora are uniform in color without the distal ends paler, so usual in many species. While this is a small species it is relatively broad. The width of the head being only 1.53 mm. but width across the mesoacetabula more than 2.73 mm. The second antennal segment is shorter than the width across head. The allotype bears the label "Java Thienemann" and is in the museum at Stockholm, Sweden. The apterous paratype female has the hind coxae slightly surpassing second abdominal segment. The male from Sumba Island, of which Dr. Lundblad gave drawings, must be the holotype and belongs to the Bogor Museum. We have not seen this but the drawing of the first genital segment of the male could not have been made from our *T. robustus* described above. Compare Lundblad's fig. 123, D (p. 391) and our fig. 9a on plate 8. Also compare the male genital hook or paramere (fig. 123, F, p. 391) and the paramere of *T. robustus* on text figure 1 in this work.

Tenagogonus pravipes Bergroth

1915 *Tenagogonus pravipes* Bergroth, E. Zool. Med. Rijks Mus. Nat. Hist., Leiden, Deel 1, 1 : 121-122 (described from Java and says that *Limnometra* Mayr is a synonym of *Tenagogonus* Stål 1855.
1933 *Limnometra pravipes* Lundblad O. Archiv für Hydrobiologie 1933, Suppl. 12, Tropische Binnengewässer 4, p. 371 (quotes Java).

The types of this species have not been located by us. Doctor Blöte says they are not at the Leiden Museum and Doctor Lindberg cannot find them in Helsingfors. We have found no specimens from Java that fit Bergroth's description which follows:

"*Tenagogonus pravipes* n. sp.

"Opacus, supra luride ochraceus, subtus pallide testaceus, linea transversa subbasali verticis, vittis duabus e petiolo communi ab illa linea emisso ortis, antrorsum levissime divergentibus, antice conjunctim basin clypei subattingentibus, vitta verticis paullo intra oculos, vitta laterali ab oculo ad basin antennae ducta, vitta curvata sublaterali pronoti antice cum vitta alterius lateris anguste cohaerente, linea media percurrente pronoti et processus ejus, linea angusta sublaterali processus pronoti paullo ante apicem ejus abrupta, vitta laterali propleurae, vitta lata partis dorsalis meso- et metapleurae, vitta laterali postice abbreviata mesopleurae, vittula ante acetabula media, margine apicali superiore horum, vittula acetabulorum posteriorum, vitta sublaterali connexivi et ventris in maculus subdissoluta articuloque ultimo nitido rostri nigris, metanoto, segmentis duobus primis dorsi abdominis suturisque dorsalibus segmentorum ceterorum hujus infuscatis, antennis et pedibus (coxis exceptis) pallide fuscis. Caput latitudine sua paullo longius, supra pilis paucis longis erectis praeditum,

fronte sat fortiter declivi, oculis antrorsum levissime convergentibus, antennis corpore longioribus, articulis primo, tertio quartoque subaeque longis, primo basin versus nonnihil curvato, secundo adjacentibus breviore, rostro medium mesosterni haud attingente. Metasternum segmentis tribus primis ventris unitis fere aeque longum, orificio prope marginem posticum posito. Abdomen (♂) parte sua dimidia dorsali coxas posticas superans, segmento ultimo dorsali duobus praecedentibus unitis parum longiore, apice truncato, segmento ultimo connexivi ultra ultimum dorsale breviter vix acute retrorsum prominulo, ventre quam dimidio mesosterni paullo longiore, parte sua pone segmentum quartum sita coxas posticas superante, segmento sexto medio duobus praecedentibus conjunctis subaeque longo, segmento genitali dorsali secundo maris perbrevi, nigricante, genitali ventrali secundo dorsale superante et quam hoc latiore. Pedum anticorum femora longiuscula, parte plus quam quarta basali nonnihil inerassata, ad apicem partis inerassatae subconstricta et subangulariter fracta, deinde usque ad apicem recta, linearia; tibiae femoribus paullo breviores; articulus secundus tarsorum primo evidenter longior. Coxae mediae marginem posticum metasterni et basin acetabulorum posticorum attingentes. Femora posteriora corpori subaequa longa. Long. ♀ 6.8 mm.

"Forma aptera: Pronotum a processu suo impressione leni transverse separatum, processu metanotum attingente, quam pronoto proprio paullo augustiore, usque ad trientem apicalem subparallelo, deinde apicem late rotundatum versus levissime angustato.

Magelang (J.).

"Extremely similar in colour to the quite inadequately described *T. anadyomene* Kirk., but it is much smaller and comparison with Ceylonese specimens of that species reveals the following important structural differences: The abdomen in *pravipes* is much shorter and not longitudinally ridged beneath in the middle, the apical angles of its last segment are much less acute, the fore legs and the second male genital segment are quite differently constructed, and the length-relations between the metasternum and the first ventral segments and between the middle coxae and the adjacent parts are different. The macropterous form of *pravipes* is unknown. In *T. anadyomene,* of which almost only the colour-markings have been described by Kirkaldy and Distant, the venter is as long as the meso- and metasternum together and longitudinally carinated in the middle, the apical angles of its last segment are very acutely produced, the second male dorsal genital segment is produced beyond the corresponding ventral segment, the fore femora are almost straight and not inerassated at the base, the fore tibiae are as long as the femora, the two joints of the fore tarsi are of equal length, the metasternum is as long as the two first ventral segments together, the middle coxae reach the middle of the metasternum but not the base of the hind acetabula, and the hind coxae barely reach the middle of the second ventral segment.

"In a paper sent for publication some months ago but not yet printed I have maintained *Limnogonus* Stål as a genus distinct from *Limnometra* Mayr, but after the study of further materials I find that *Limnogonus* cannot be considered even subgenerically distinct, as the transitions in the mutual length of the two joints of the fore tarsi and in the shape of the apical angles of the last abdominal segment are too numerous. *Limnometra* is a synonym of *Tenagogonus* Stål, the type of which is *T. albovittatus* Stål (1855) from Natal, a species totally for-

gotten by Stål himself in his later writings and also omitted in the Catalogue of Lethierry and Severin.

"N. B.—The segment following immediately after the metanotum has by me previously (Ent. Monthly Mag. 1902, p. 259) been called the metaphragma, but I now with Breddin think it more natural to regard it as the first abdominal segment."

Tenagogonus pravipes bergrothi subsp. nov.

(Pl. 2, fig. 10; Pl. 8, fig. 8)

Size: Winged male 7.56 mm. long; width across the mesoacetabula 2.42 mm.; width across head 1.36 mm. Small wingless male: 5.04 mm. long; width across mesoacetabula 1.76 mm.; width across head 1.16 mm. Winged female 6.93 mm. long; width across mesoacetabula 2.35 mm.; width across head 1.3 mm.; wingless female: 6.6 mm. long; width across mesoacetabula 2.52 mm.; width across head 1.28 mm.

Color: General color light yellowish-brown. Head and pronotum yellowish brown with the dark reddish-brown to black figures as shown in the illustrations. Black band on propleuron behind eye, continued as two broad bands on mesopleuron, the upper one broader, ending on the metaacetabula and the lower one turning down and ending before reaching the dark band on mesoacetabula. Venter light, nearly white except for a dark spot on metasternum and underside of connexicum embrowned.

Structural characteristics: Proportional length of antennal segments of winged male: 1st: 2nd: 3rd: 4th:: 85: 83: 106: 108, total length of antenna 8.02 mm. Beak moderately slender, covering less than one third of mesosternum. Front femur slightly, if any, stouter than middle femur.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	130	114	13	22
Middle leg	300	235	108	27
Hind leg	270	145	30	25

In winged form, shape of pronotum and venation of hemelytra as shown in the illustration. In the apterous form the shape of pronotum is shown for a female and is relatively broader than in male. Connexivum moderately broad, male without connexival spines and female has the outer angle of connexivum produced almost into a spine. Dorsal abdominal segments of the male fairly short, last one not as long as the two preceding ones. Hind coxae

of male surpassing rear margin of second abdominal segment; of the female reaching or surpassing the middle of second ventral abdominal segment. Last ventral abdominal segment of female shorter than the two preceding segments. In the male the last ventral abdominal segment shorter than the two preceding segments and together with genital segments almost as long as the rest of the abdomen. The venter of first genital segment of the male with a median longitudinally depressed line. Male genital capsule without lateral hair tufts.

Location of types: Described from fifteen males (five winged) and twenty females (one winged) labeled "Observatory Garden, Manila, P. I." and two females labeled "Mainit, Surigao Mindanao, P. I. III, 21, 31, A. C. Duyag". The last two belong to California Academy of Sciences. Others are from Bueno coll. in the University of Kansas collection. Holotype and allotype wingless. Holomorphotype and allomorphotype are winged.

Comparative notes: As in *Tenagogonus pravipes* Bergroth the males have the basal third of the front femur somewhat thicker and then curved beyond. This is not true for *T. robustus* sp. nov. or for *T. brevis* (Lundblad) which are closely related species.

Data on distribution: Known only from the type series above. We have a species from the Philippines that must be very close to *Tenagogonus pravipes* Bergroth. In some respects it does not agree with Bergroth's description and since he did not mention the striking impressed line on the venter of the first genital segment of the male we are describing it as a subspecies.

Tenagogonus fijiensis sp. nov.

(Pl. 2, fig. 9; Pl. 8, fig. 7)

Size: Apterous male: 5.25 mm. long; width across mesoacetabula 2.41 mm.; width across head 1.51 mm. Apterous female: 6.72 mm. long; width across mesoacetabula 2.73 mm.; width across head 1.74 mm.

Color: Head reddish brown with two longitudinal black lines meeting at both ends, a black band along each eye; pronotum reddish brown, with a median longitudinal black line, broader on anterior lobe, lateral black lines near the margin that are very broad on anterior lobe; black band on propleuron behind eye and continued as two bands separated by a pale stripe; the upper band ending on the metaacetabula and the lower one on the mesoace-

tabula. Underside of male connexivum embrowned, venter otherwise pale.

Structural characteristics: Proportional length of antennal segments of male: 1st: 2nd: 3rd: 4th:: 92: 64: 62: 70. Total length of antenna 6.05 mm. Beak moderately stout and short for this genus. Front legs stout, femur much thicker than middle femur.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	125	115	14	20
Middle leg	280	262	74	23
Hind leg	290	170	27	17

Pronotum of the apterous form narrowed at caudal end. Connexivum of female, erect on basal segments and reflexed on distal segments, with the caudal angles produced and overlapping. Connexivum of male semierect, no connexival spines, its dorsal abdominal segments short except the last one which is as long as the two preceding segments and as long as the first genital segment. Ventrally, hind coxae of male surpass the rear margin of the fourth abdominal segment; in female they surpass the rear margin of the second. Ventral abdominal segments of male short except last one, which together with the genital segments is longer than rest of abdomen. The ventral surface of first genital segment normal. Last ventral abdominal segment of female as long as three preceding segments, tubular, ending in a mid-ventral point.

Location of types: Described from holotype, allotype and two male paratypes labeled "Fiji Islands, July 1934 R. W. Paine" "Taveuni; Ura. Stagnant pool in rocky stream bed of forest 2500 ft." (K. U. coll.)

Comparative notes: The shape of the pronotum in these apterous insects and the tubular last ventral abdominal segment of the female are characteristic.

Tenagogonus kuiterti sp. nov.

(Pl. 2, fig. 11; Pl. 9, fig. 11)

Size: Winged male: 10.37 mm. long; width across humeri 2.1 mm.; width across mesoacetabula 2.83 mm.; width across head 1.64 mm. Apterous male: 8.74 mm. long; width across mesoacetabula 2.77 mm.; width across head 1.55 mm.; apterous female: 8 mm. long; width across mesoacetabula 2.63 mm.; width across head 1.43

mm. The size shows considerable variation. Winged males may be only 7.98 mm. long and apterous males only 6.3 mm.

Color: General color light brown. Head and pronotum light brown with the dark reddish brown to black figures as shown in the illustration. Note the pale spot on inner margin of hemelytron in winged forms. Dark brown to black band on propleuron behind eye continued as two bands on mesopleuron, the lower one broader and often broadened in one or two places to join the upper band, usually ending free but occasionally joining the upper of two spots in the mesoacetabula. Venter pale except for a black spot at anterior end of the mesoacetabular cleft and underside of the connexivum embrowned.

Structural characteristics: Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 90: 83: 108: 100. Total length of antenna in this wingless male 8 mm. this male being 6.55 mm. long. Beak moderately slender, not covering one third of mesosternum. Front femur of male slightly stouter than middle femur.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	118	100	13	20
Middle leg	290	215	95	30
Hind leg	290	125	24	24 including claws

Winged form: shape of pronotum and venation of hemelytron as shown in the illustrations. In apterous male the shape of pronotum is shown and also in a slightly brachypterous male, the wing pads too short to be exposed. The male with very short connexival spines, especially in apterous forms. Female with broad connexivum and short spines. Last dorsal abdominal segment of male not as long as the two preceding segments but longer than the dorsum of the first genital segment. In female last dorsal abdominal segment as long as the next preceding segment. Ventrally the male abdomen nearly as long as mesosternum. First genital segment of male with lateral transverse depression, its venter normal.

Location of types: Described from eleven males (three winged) and three females from "Mohnyin, Burma X. 27. 1944 L. C. Kuitert" and "Burma, 1944. L. C. Kuitert" in the University of Kansas collection.

Comparative notes: This species we are placing in *Tenagogonus* Stål because it has so many characters of that genus. It is the only

species with connexival spines but they are very short and variable, almost absent in some wingless males.

Data on distribution: Besides the type series we have 1 male and 4 females bearing the label "Shingbwiyang, Burma XI-15-1944 Capt. L. C. Kuitert". These are all winged specimens and their connexival spines are evenly developed.

Genus *Limnometra* Mayr

1865 Mayr, Gustav L. Verh. Zool-bot. Ges. 15: 443. (New genus for: *L. femorata* Mayr and six other species.)
1865 Mayr, Gustav L. Reise der österreichischen Fregatte Novara Expedition um die Erde. Zool. Theil 2 (1): 174 Wien. (Key to species.)
1909 Kirkaldy G. W. and Torre Bueno, J. R. de la. Proceedings of Ent. Soc. Washington 10: 209. (Given as synonym of *Tenagogonus* Stål.)
1915 Bergroth, E. Zool. Med. Rijks Mus. Nat. Hist., Leiden 1 (2): 121-123. (Gives *Limnometra* Mayr as synonym of *Tenagogonus* Stål 1853.)
1925 China, W. E. Bull. Brooklyn Ent. Soc. 20: 218. (Revives *Limnometra* Mayr for *L. gigas.*)
1933 Lundblad, O. Archiv für Hydrobiologie. Suppl. 12. "Tropische Binnengewässer 4," p. 371.

Medium to large elongate gerrids with moderately long antennae, middle and hind legs. Male abdomen longer than the mesosternum. Last male ventral abdominal segment plus the genital segments shorter than the preceding four ventral abdominal segments. First tarsal segment of the front leg usually longer than the second. Abdominal spiracles closer to the anterior margin of the segments. Males with connexival spines or with connexivum produced into a triangular flattened plate. Hind coxae not covering second ventral abdominal segment. Metasternum equal to or shorter than first two ventral abdominal segments. Last ventral abdominal segment of male equal to or shorter than preceding segment. In Limnometra the males are often larger than the females.

Limnometra minuta Mayr

(Pl. 2, fig. 13; Pl. 10, fig. 14)

1865 *Limnometra minuta* Mayr, Gustav L. Verh. Zool.-bot. Vereins, Wien, 75: 444.
1865 *Limnometra minuta* Mayr, Gustav L. Hemiptera in Novara Expedition, Zoolog. Theil, Wien, 2 (1): 175, 176-177. figs. 54a, 54b. (Gives additional description and figures.)
1904 *Gerris minuta* Distant W. L. The Fauna of British India Rhynchota 2: 181. (Quotes Nicobar Islands.)
1933 *Limnometra minuta* Lundblad, O. Archiv für Hydrobiologie, Suppl. 12. "Tropische Binnengewässer 4", p. 371, 373.

The type of this species is a winged male bearing the label "Novara Exp. Sambelong". It fits perfectly Mayr's two descriptions and notes. While mostly a color description he gives the length (8.6 mm.), thus smaller than the other species he knew, the nonciliated

middle femora and the broadly based triangular connexival spines, which are useful in recognizing this species; yet one hundred years have passed without any one recognizing additional specimens. Surely on some Nicobar Island this species still exists. The following notes and drawings of the type may be helpful in recovering this much desired little species.

Notes on *Limnometra minuta* Mayr:

Size: Type is a winged male, 8.61 mm. long; width across humeri 1.47 mm.; width across mesoacetabula 2.1 mm.

Color: Color pattern not striking. Antennae and legs of uniform color with part of tarsi darker. Antennae darker than the legs. Head has a nearly black tylus; just back and laterad of the tylus stripe are light brown lines that converge and unite into a median stripe at the anterior level of the eye emarginations; there is another brown line near the inner margin of eye that unites in front with the mediolateral band, thus producing an M-shaped figure on head; a dark band between the base of antenna and eye. Pronotum has a median longitudinal, nearly black line and another separated from the lateral and caudal margins by a pale line; on the anterior lobe, on either side, between the dark lines is a light brown streak that fades out before the level of humeri; a brown streak on side of prothorax behind eye, this is continued as a dorsolateral streak on mesothorax. There is a dark-brown elongate spot on anterior acetabula, two curved ones on middle acetabula and one on the posterior acetabula. There is a faint brown lateral streak on mesothorax and a black spot at anterior end of mesoacetabular cleft. Venter pale. Last segment of the beak shining, black. Hemelytra brown.

Structural characteristics: Antennae slender. Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 93: 73: 98: 133. The total length of this antenna is 8.32 mm. Front femur somewhat curved and about twice as thick as tibia. The segmental formula: Femur: tibia: 1st tarsal: 2nd tarsal:: 133: 115: 17: 18. Middle femur measures 6.93 mm. long and has neither cilia nor pegs. Other segments are gone. Metasternum about equal to first two abdominal segments. Abdominal venter with faint median carina. Male genital segments about as long as the last two ventral abdominal segments. The abdominal sides parallel as seen from beneath and the connexival spines are very broad at base, triangular in shape and not quite reaching the tip of the body. We have seen no other species with connexival spines like this.

Limnometra lipovskyi sp. nov.

(Pl. 3, fig. 20; Pl. 9, fig. 12)

Size: Winged male: 13.44 mm. long; width across humeri 2.47 mm.; width across mesoacetabula 3.78 mm.; width across head 2.14 mm. Winged female: 10.9 mm. long; width across humeri 1.93 mm.; width across mesoacetabula 3 mm.; width across head 1.84 mm. Wingless forms probably smaller, since one wingless male is only 7.35 mm. long.

Color: General color pattern quite distinctive, yellowish brown and black. The black figures as shown in the illustration. Dark brown to black band on propleuron behind eye as usual but the upper band on mesopleuron almost obliterated, only the lower one which is dark brown is present and it fades out before reaching mesoacetabula. Males have a longitudinal black line on basal third of middle femur while females have a short black spot near base as do *L. ciliata* Mayr. Venter is pale.

Structural characteristics: No male has an entire antenna. One with three segments gives the following proportional lengths: 1st: 2nd: 3rd: 4th:: 150: 145: 130: ?. A female antenna: 1st: 2nd: 3rd: 4th:: 120: 100: 90: 100. Beak moderately slender but not covering one third of mesosternum. Front femur of male not stouter than middle femur.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	255	230	35	33
Middle leg	710	700	191.9*	34.9*
Hind leg	760	432	65	25

The middle femur and tibia of male have, ventrally, a wide brush of scattered cilia. Winged form: Shape of pronotum and venation of hemelytra as shown in illustration. Male with very short connexival spines that are probably more reduced in apterous forms; last abdominal tergite longer than preceding one but shorter than the first genital segment; ventrally the male abdomen longer than the mesosternum; last ventral abdominal segment slightly shorter than preceding one; venter of first genital with stout lateral protuberances arising from its venter. Last venter abdominal segments of female as shown in the drawing.

Location of types: Described from three winged males and four winged females labeled "Guadalcanal 1944. L. J. Lipovsky" and

* Calculated from smaller male.

one female "Guadalcanal 1945. P. H. Eschmeier". All of these are in the University of Kansas collection.

Comparative notes: This species, like *L. kuiterti* has very short connexival spines. The protuberances on the venter of the first genital segment of the male distinguish this species.

Data on distribution: Known only from Guadalcanal.

Limnometra octopunctata Hungerford

(Pl. 4, fig. 22; Pl. 10, fig. 13)

1955 *Limnometra octopunctatus* Hungerford, H. B. Journal Kansas Ent. Soc., 28: 67-68.

Size: Apterous male: 9.24 mm. long; width across the mesoacetabula, 2.625 mm. Apterous female: 11.25 mm. long; width across the mesoacetabula, 3.25 mm.

Color: Reddish brown above, lighter beneath; head with a broad median brown band that is wider in front and bordered by lighter narrower lines; pronotum with a median black band that is broad in front and tapering on the anterior lobe to a slender line that continues on the posterior lobe to its apex; the posterior lobe with a slender lateral submarginal black line to the shoulders where it broadens and is bordered by a pale line around the apical lobe; behind the pronotum is a median brown to black band that continues to abdominal tip; on this dark band from the third abdominal segment to the eighth there is a median series of gray streaks; on each acetabulum, a pair of black spots; between these spots a small creamy white spot on the mesoacetabulum and on metaacetabulum a large triangular creamy white spot. On the venter eight large nearly round black spots that characterize the species and suggest the name. These spots are located as follows: One black spot in front of and one on the venter beneath each mesoacetabulum, one beneath each metaacetabulum and another on either side of the last abdominal segment. On each side of the first genital segment of the male there is another black spot half hidden beneath the last abdominal segment. If such spots are also on the female they are entirely hidden.

Structural characteristics: The male has lost the last two segments of its antennae. The length of the first and second segments are respectively 2.6 mm. and 2.73 mm. so the second is longer than the first. The female also is imperfect and only one antenna is represented by three segments that measure: 1st, 2.52 mm.; 2nd, 2.14 mm.; 3rd, 2.18 mm. The beak is moderately long (3.21 mm.),

elongate third segment reaching back some distance on mesosternum. The relative lengths of the segments of the beak are 1st: 2nd: 3rd: 4th:: 30: 13: 90: 21 (♂). Fourth segment black and shining and its mean diameter about half that of the third which is slender and its diameter about half of the first segment. Front legs of both sexes have the basal two thirds of femora thickened. The relative lengths of the segments, femur: tibia: 1st tarsal: 2nd tarsal:: 167: 137: 23: 23 (♂) and 180: 155: 30: 30 (♀). Middle legs long, femur being 9.24 mm. long in male and 10.3 mm. in female; the relative lengths of the segments, femur: tibia: tarsus:: 440: 410: 120 (♂) and 490: 466: ? (♀); hind legs shorter than middle legs; the hind femur of the male 9.24 mm. long and that of female 10.25 mm.; the relative lengths of the male segments being, femur: tibia: tarsus:: 440: 217: ?; for the female 488: 290: 70. In the male connexival spines reaching about three fourths the length of first genital and in the female surpassing the first genital and extending half the length of the last genital. Ventrally the rear margin of the first genital segment of the male has laterally on each side a projection.

Location of types: Described from holotype male and allotype female and one male paratype bearing the label "Dr. B. Hagen, Tandjong Morawa. Serdang. (N. O. Sumatra.)" These are in the Francis Huntington Snow Museum, University of Kansas.

Comparative notes: The eight distinct black spots on the venter will identify this species. The lateral angular projections on the rear margin of the first genital segment of the male appear to relate it to *L. ciliatus,* Mayr. It also has the ciliate row on the rear margin of the middle femur but not as conspicuous as in *L. ciliata* and is a smaller species.

Limnometra fluviorum (Fabricius)

(Pl. 3, fig. 19; Pl. 10, fig. 15)

1798 *Gerris fluviorum* Fabricius, J. C. Ent. Syst. Suppl. 543. 2. (Described from Tranquebar in Tanjore Dist. India.)
1803 *Hydrometra fluviorum* Fabricius, J. C. Syst. Rhyn. p. 257.
1865 *Limnometra fluviorum* Mayr, Gustav L. Hemiptera in Novara Expedition Zool. Theil, Wien. 2 (1): 175.
1868 *Limnometra fluviorum* Stål, C. Hemiptera Fabriciana p. 132.
1904 *Gerris fluviorum* Distant, W. L. The Fauna of British India. Rhynchota 2: 177. (Records: Pondicherry [coll. sign]). Bombay; Bor. Ghat (Dixon). Trivandrum, (Brit. Mus.) also records Java and Bourbon Isl.
1914 *Limnometra fluviorum* Horváth, G. Ann. Mus. Hung. 2: 660.
1933 *Limnometra fluviorum* Lundblad, O. Archiv. für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4" p. 371. (Gives Vorderindien, Ceylon, Java. ? Reunion.)

We believe the following to refer also to this species:

1840 *Gerris armata* Spinola, Maximilien, Essai sur les Insectes Hémiptères, p. 65. This is described from Bombay and is characterized by the spine on the intermediate coxa in both sexes as is *L. fluviorum*.

1904 *Gerris armata* Distant, W. L. The Fauna of British India Rhynchota 2: 180-181. This species is from 10 to 13 mm. long, rather heavily banded with black. The antennae and legs are not annulated. The front tarsal segments with the second segment longer. The mesocoxal spine will identify this species.

Location of type: Daldorff collection at the Zoological Museum, Copenhagen, Denmark.

Data on distribution: This was described from Tranquebar, India and Lundblad records Ceylon and Java.

We have before us the following: "India, Tanjore Dist. P. S. Nathan". 1 male, 1 female. (K. U.); "India, Tanjore Dist. Nedungadu P. Susai Nathan". 2 males, 2 females. (Basel Mus.); "India, Coimbatore Dist. P. Susai Nathan". 2 females. (Basel Mus.); "South India. Coimbatore 6. VI 1950, P. S. Nathan". 1 male, 1 female. (K. U. coll.); "Coimbatore, India". 1 male. (Calif. Acad. Sci.); "Coromandel, M. Maindron". 3 males, 3 females. (Kirk. coll. K. U.); "Chikkaballapura, S. India T. V. Campbell". 1 female (K. U.); "Kurumbagaram, Karikal Terr. S. India 16-IV-47 coll. P. S. Nathan". (coll. of H. S. Wallace No. 1706.) 1 male.

Limnometra anadyomene (Kirkaldy)

(Pl. 5, fig. 30; Pl. 11, fig. 16)

1901 *Gerris (Limnometra) anadyomene* Kirkaldy, G. W. Entomologist 34: 117. (Desc. from Punduloya, Ceylon colls. E. E. Green and Kirkaldy.)
1904 *Gerris anadyomene* Distant, W. L. The Fauna of British India. Rhynchota 2: 177-178. (Records Ceylon; Punduloya [Green]—Philippine Islands [Simon]).
1915 *Tenagogonus anadyomene* Bergroth, E. Zool. Med. Rijks Mus. Nat. Hist. Leiden, Deel 1. 2: 122.
1933 *Limnometra anadyomene* Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4" p. 371. (Gives Ceylon, Hinterindien, Philippinen.)

The following is Kirkaldy's brief description:

"*Gerris anadyomene* sp. nov.

Belongs to subgenus *Limnometra* Mayr. Flavous, head with an irregular diamond and two lateral stripes, pronotum with a median and two sublateral lines, irregular markings on ambulacra, etc. black. Elytra dark greyish fulvous; nervures fulvous, apically darker. Spines of seventh segment extending beyond apex of abdo-

men, eyltra extending far beyond apex of abdomen. Male: seventh segment deeply, roundly emarginate ventrally. Leng. to apex of elytra 11 mm. Ceylon, Punduloya. Collns. E. E. Green and Kirkaldy. Larger and stouter than *minuta* (Mayr) to which it is somewhat allied."

We have before us Kirkaldy's type series bearing the label "Punduloya Ceylon. E. E. Green". There are twenty-five specimens, three of them winged. In only one of the eight males do the connexival spines slightly surpass the tip of the abdomen. In all females they are shorter. Therefore his statement is misleading. The following brief notes may be helpful in recognizing this species.

Size: Length: 9 mm.-14 mm.; width across mesoacetabula: male 2.73 mm., female 3.61 mm.; width across eyes: male 1.64 mm. female 1.72 mm.

Color: General color medium to light reddish brown especially in apterous forms. The lateral pronotal dark band continuous over the humeri in apterous forms, but often obliterated at tip. Antennae and legs uniform in color, not annulated. Each dorsal abdominal segment in apterous forms with two more or less, crescent-shaped dark bands, embracing a paler spot. Underside of connexivum usually dark. Venter light.

Structural characteristics: Proportional length of antennal segments of male: 1st: 2nd: 3rd: 4th:: 118: 87: 108: 120; of female: 113: 72: 96: 110. Total length about equal to body length in male, less than body length in female. Front femur not thicker than middle femur, the second tarsal segment longer than the first. Middle femur longer than the body in male, about equal in female. Connexival spines of the male usually surpass the first genital segment but seldom surpass the abdominal tip, and never do so in the female.

Location of types: The types mentioned above are in the Kirkaldy collection in the Francis Huntington Snow Entomological Museum, University of Kansas.

Comparative notes: In this species the females are strikingly broader and larger than the males. Its nearest relative appears to be *L. kuiterti* which has shorter connexival spines in the male.

Data on distribution: Described from Ceylon and Dr. Lundblad records "Philippines" and "Hinterindien".

We have before us the following:

Ceylon: Kirkaldy's type series "Pundaloya, Ceylon E. E. Green". 8 males, 17 females (Kirk. coll. K. U.); "Süd Ceylon, Mai 1889 H.

Fruhstorfer" 1 male, 1 female (K. U.); "Suduganga River, Matale, Ceylon, R. A. Senior-White" 4 males, 6 females, 4 nymphs. (Bueno coll. K. U.); "Woodside, Ungalla, Ceylon 3.IX.22. 1 male (Brit. Mus.).

S. Shan States: "Heho, 3800", Yawagheve, S. Shan States 7. III, 17, Gravely. 2 males. (Bueno coll. K. U.)

Limnometra insularis sp. nov.

(Pl. 4, fig. 21; Pl. 11, fig. 17)

Size: Winged male type 11.76 mm. long; width across humeri 1.78 mm.; width across mesoacetabula 2.52 mm.; width across head 1.64 mm. Winged female 9.77 mm. long; width across humeri 1.68 mm.; width across mesoacetabula 2.63 mm.; width across head 1.64 mm.

Color: Yellowish brown, the dark markings reddish brown to black, and limited as shown in the illustration. Head markings faint, the holotype having a faint M-shaped figure. Median longitudinal pronotal stripe with pale band on either side, last two or three antennal segments white. Distal ends of middle and hind femora not pale. Dark band on propleuron close to lateral pronotal band separated by the cream colored marginal band and continued on mesopleuron. One or two brown spots on all three acetabula. Venter pale. Mesosternum partially pubescent.

Structural characteristics: Proportional length of antennal segments of the Holotype from N. O. Sumatra: 1st: 2nd: 3rd: 4th:: 125: 103: 133: 155. Total length of antenna 10.8 mm., one male with body length 11.76 mm. Beak moderately slender, covering a little more than one fourth of mesosternum. Front femur of male slender, not thicker than middle femur. Middle femur of male without a definite fringe of cilia beneath but with many minute spicules. Mesosternum of male almost bare.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	172	145	30	27
Middle leg	460	400	130	27
Hind leg	525	260	50	22

Winged form: Shape of pronotum and venation of hemelytra as shown in the illustration, typical for *Limnometra* species. Connexival spines surpassing genital segments in both sexes. Last ventral abdominal segment of male plainly shorter than preceding

segment, in female slightly longer. The median ventral longitudinal keel indistinct on last abdominal segment or two.

Location of types: Described from holotype male labeled "Dr. B. Hagen, Tandjong Morawa. Serdang, N. O. Sumatra". Allotype female labeled "Ardjeano, Java" and a paratype male bearing the same label, a female labeled "Chan Yoma, Birmanie" and a male from "Pulo Laout," an island near Borneo.

Comparative notes: This species looks like *L. borneensis* sp. nov. but differs greatly in the shape of the front femur of the male, in the proportions of the leg segments and in lacking the fringe of cilia on the middle femur of the male.

Data on distribution: The type series includes Sumatra, Java, Burma? and the island of Pulo Laout.

Limnometra palauana Esaki

(Pl. 3, fig. 16; Pl. 12, fig. 18)

1925 *Limnometra palauana* Esaki, T. Philippine Jour. Sci. 26, 1: 57.
1933 *Limnometra palauana* Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4" p. 371. (Records Palau Isl.)
1937 *Limnometra palauana* Esaki, T. Tenthredo 1, 3: 362. (Species occurs only on the Island group of Truk but not in Palau Islands on which the specific name was erroneously created.)

Original description: "Body dark yellowish brown. Head dark yellowish brown, with a somewhat indistinct black fascia along the inner margin of eyes; apex black and shining; fasciae on vertex very obscure. Antennae dark brown. Pronotum dark yellowish brown, with the central and marginal lines black; margin and the area along the central median black line yellow. Hemelytra dark yellowish brown, veins much darker. Legs dark yellowish brown. Undersurface of body pale yellowish brown, with two longitudinal black fasciae on mesopleura. First and fourth joints of antennae subequal in length, second about two thirds of first, third a little shorter than first. Length of body: male 9 mm.; female 11 mm. Holotype (male), allotopotype (female), and paratopotypes collected on Jan. 8, 1915, on Palau Island, Micronesia, by S. Fujita; presented by S. Matsumura; in my collection."

This species is nearly allied to *Limnometra annulicornis* (Breddin) from Celebes in shape and coloration, but is much smaller, and the markings on the vertex are much more obscure. The color description would apply to a half-dozen species, the size is within the range of several species, the antennae are variable in many cases, and that leaves the description of the antennal segments the only structural character. Fortunately, Dr. Esaki kindly sent us three

specimens, two females bearing the label "Caroline Islds, Truk: Toloas 21, 1, 1938 Teiso Esaki" and one male "Caroline Islds, Truk: Toloas-Erin-16 XI 1937 Teiso Esaki", all labeled by him "*Limnometra palauana* Esaki". The antennae and legs were mostly free in the bottom of the box but we submit what details we can concerning this species. The fully winged female is 8.82 mm. long; the short winged female 8.19 mm. The male is also short winged, also with complete venation as in the female but the abdomen was free in the box. Both sexes have well-developed connexival spines reaching approximately to the caudal tip of the body. The hind coxae of the male reaching slightly beyond the rear margin of the first abdominal segment and barely reaching it in the female. The abdominal spiracles are nearer to the anterior than to the posterior margins of the segments. The abdominal venter is longer than the mesosternum and typically that of a *Limnometra*. The front femur of the male is thicker than that of the female and is hairy beneath. The first tarsal segment is longer than the second in both sexes. The one unbroken antenna that was free in the box has the antennal formula as follows: 1st: 2nd: 3rd: 4th:: 90: 55: 66: 90, its total length 6.3 mm. The antenna is slender and shorter than the insect but over half its length. The front leg of the male has the following measurements: Femur, 155 spaces long, 22 spaces at greatest diameter; tibia 128 spaces; 1st tarsal 20 spaces; 2nd tarsal 16 spaces. The front leg of a female: Femur 140 spaces long, 14 spaces greatest diameter; tibia 120 spaces; 1st tarsal 30 spaces; 2nd tarsal 17 spaces. The middle femur of the fully winged female is a little larger in diameter than the hind femur and measures 315 spaces or 7.6 mm. long. The middle tibia 280 spaces, 1st tarsal 90 spaces, 2nd tarsal 23 spaces. The hind femur is broken but identifiable and measures 340 spaces long, the tibia 180 spaces, 1st tarsal 37 spaces, 2nd tarsal gone. The rather angular, unevenly thickened front femur with its heavy layer of hair beneath will separate the male of this species from others of similar size and general appearance. Its closest relative appears to be *L. borneensis*, from which it differs in having a broader median black line on the pronotum and the middle and hind femora not being paler at the tips.

We also have a series labeled "Los Negros, Admirality Islds. 11-8-45 P. T. Richard 174". 9 males, 2 females (U. S. N. M.) that are a little larger, with slightly longer connexival spines and less thickened front femora in the males. This probably represents variation within the species. See pl. 3, fig. 17 and pl. 16, fig. 28.

Limnometra borneensis sp. nov.

(Pl. 2, fig. 12; Pl. 12, fig. 9)

Size: Winged male: 10 mm. long; width across humeri 1.89 mm.; width across mesoacetabula 2.6 mm.; width across head 1.47 mm. Winged female 9.78 mm. long; width across humeri 1.89 mm.; width across mesoacetabula 2.64 mm.; width across head 1.38 mm.

Color: Yellowish brown, the dark markings dark reddish brown to black, and limited as shown in the illustration. Head with faint line near inner margin of eye, the median longitudinal pronotal stripe slender and the pale band on either side indistinct. Tip of last antennal segment probably white; distal ends of middle and hind femora pale. Dark band on propleurum close to the lateral pronotal band separated by the cream-colored marginal band; practically no color markings on mesopleuron. Venter pale.

Structural characteristics: Proportional length of antennal segments of male: 1st: 2nd: 3rd: 4th:: 83: 43: 60: 95. The antenna of the female is 5.84 mm. long, her body 9.78 mm. long. Beak moderately slender, rather short, only covering one fourth of mesosternum. Front femur of the male thicker than middle femur and broadest beyond its middle. Middle femur of male with fringe of short cilia beneath. Mesosternum of male without long cilia, with only short pubescence.

The relative length of leg segments:

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	156	130	24	22
Middle leg	415	335	?	?
Hind leg	390	270	82	26

Winged form: Shape of pronotum and venation of hemelytra as shown in the illustration, typical for *Limnometra* species. Connexival spines surpassing genital segments in both sexes. Last ventral abdominal segment of male slightly shorter than preceding segment, in female slightly longer. The median ventral longitudinal keel prominent on all abdominal segments.

Location of types: Described from two males and two females labeled "Mt. Pol, Sarawak, Borneo. Mjöberg collection, W. W. Funge Begnest" in California Academy collection.

Comparative notes: The color pattern and the shape of the front femur of the male are the distinctive features of this species. Its closest relatives appear to be *L. palauana* Esaki and *L. rossi* sp. nov.

Data on distribution: Besides the types we have a pair from "Mt. Murud, Borneo. Mjöberg collection W. W. Funge" that are larger, the winged male being 14.3 mm. long but the front femur of the male is like the type. The antennae are entire and more definitely white at tip.

Limnometra rossi sp. nov.

(Pl. 3, fig. 18; Pl. 12, fig. 20)

Size: Winged male: 6.9 mm. long; width across humeri 1.36 mm.; width across mesoacetabula 1.9 mm.; width across head 1.18 mm. Winged female: 7.56 mm. long; width across humeri 1.5 mm.; width across mesoacetabula 2.23 mm.; width across head 1.26 mm.

Color: Rather dark compared with similar species because there are numerous figures of dark brown or black as shown in the illustration. The dark bands on the connexival segments are rather striking. The black band on propleuron is broad and divides on mesopleuron into two narrow bands, the upper one along the upper edge and ending at the spiracle and the lower one, an undulate line that ends at base of mesoacetabula. The brown band across the margin of the proacetabula is continued on the mesothorax to end before reaching anterior end of mesoacetabular cleft. Two brown spots on meso- and metaacetabula. Underside of connexivum with dark spots often joined into a solid band. Venter otherwise pale. Antennae, middle and hind femora not annulated.

Structural characteristics: Proportional length of antennal segments of the male holotype: 1st: 2nd: 3rd: 4th:: 70: 45: 65: 100. The total length of the antenna is 5.88 mm. and the insect 6.9 mm. long; of the female: 1st: 2nd: 3rd: 4th:: 73: 38: 60: 103. The total length of antenna is 5.67 mm. and the insect 7.56 mm. long. Beak slender covering not quite one third of mesosternum. Front femur of male much thicker than middle femur and broadest beyond its middle. Middle femur of male with fringe of short cilia beneath. Mesosternum of male with very short pubescence.

The relative length of leg segments.

	Femur	*Tibia*	*First tarsal segment*	*Second tarsal segment*
Front leg	90	93	15	16
Middle leg	250	208	90	26
Hind leg	265	127	40	18

Winged form: Shape of pronotum and venation of hemelytra as shown in illustration. Connexival spines barely reaching tip of genital segments. Last ventral abdominal segment of male equal

in length to preceding segment, in female somewhat longer. Median ventral longitudinal keel on abdominal segments present but not prominent.

Location of types: Described from ten males, nine females from "San José, Mindoro, Philippine Islands, E. S. Ross." These were taken on various dates from January to April, 1945. The holotype male, allotype and some paratypes in the California Academy of Sciences and some paratypes in University of Kansas collection.

Comparative notes: The checkered pattern of the connexivum separates this species at a glance from its relative *L. borneensis* sp. nov.

Data on distribution: Known only from the type series from the Philippines.

Limnometra ciliata Mayr

(Pl. 3, fig. 14; Pl. 13, fig. 22)

1865 *Limnometra ciliata* Mayr, Gustav L. Verh. zool-bot. Vereins, Wien, 15: 444.
1865 *Limnometra ciliata* Mayr, Gustav L. Hemiptera in Novara Expedition Zool. Theil, Wien, 2 (1): 174. (Places in his key to species.)
1908 *Limnometra ciliata* Kirkaldy, G. W. Proc. of Linn. Soc. of N. S. Wales. 33: 367. (Records Viti Levu, in a catalogue of the Hemiptera of Fiji.)
1933 *Limnometra ciliatus* Lundblad, O. Archiv. für Hydrobiologie, Suppl. 12. "Tropische Binnengewässer 4," p. 371. (Records Java, Fidschi?, Molukken?)
Also referring to the above species:
1865 *Limnometra inermis* Mayr, Gustav L. Verh. zool.-bot. Vereins, Wien. 15: 444. (Desc. from Manila but the type is a female, not a male and is the only specimen in the Vienna Museum determined by Mayr as *inermis*. It also bears the label "Novara Exp. Manila." (See Plate 3, fig. 15a.)
1865 *Limnometra inermis* Mayr, Gustav L. Hemiptera in Novara Expedition Zool. Theil, Wien, 2 (1): 174. (Places in his key to *Limnometra* and gives about the same Latin description as above but records "Manilla auf Luçon" and follows with a longer description in German.)
1933 *Limnometra inermis* Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4," p. 371.

Mayr described this species as follows:

"*L. ciliata* n. sp. ♂ long. 19.5 mm. Fulva, pronoto nigro lineato, capite supra linea mediana lata et lineis 2 lateralibus angustis, acetabulus pedum intermediorum muticis, pedibus fuscis, femoribus intermediis ante apicem absolute inermibus, intus long ciliatis. —Java."

While the above description is short, the large size, the unarmed but densely ciliated middle femur led Kirkaldy 1908 to record the species from "Viti Lavu" in the Fiji Islands. However, since *Limnometra cursitans* (Fabricius) from Australia is also a large species with ciliated middle femur it is necessary to give additional notes on both species. Fortunately, there are good structural characters that separate these species.

Notes on *Limnometra ciliata* Mayr.

Size: Mayr give the male as 19.5 mm. long. Since the males are often larger than the females in certain species of *Limnometra* it is not surprising to find the average size of this species to be less than 19.5 mm. We have examined specimens of this species from the Philippines to the Fijis and found the length varies from the large male type from Java 19.5 mm. to a small male from Fiji only 13 mm. long. We have other males from Fiji 17.5 mm. long. A male from Ternate is 19 mm. long. In the series from Guadalcanal the largest male is 18.9 mm. long, while the largest female is 14.2 mm. long.

Color: Typical color pattern is shown on Plate 3. The colors are brown and black varying from forms having pronotum and hemelytra mostly black to forms where brown is dominant. Venter is pale. Antennae and legs uniformly brown without pale annulations. On base of middle femur a short black streak.

Structural characteristics: The segmental formula for the antenna is not constant even for individuals from the same place. For example the antennal measurements for four specimens, taken at the same time and place in Guadalcanal are as follows:

1st:	2nd:	3rd:	4th	
245:	193:	145:	125	♂
222:	168:	136:	122	♂
156:	122:	100:	100	♀
160:	127:	110:	112	♀

Front femur of male is nearly straight and slender, not thicker than middle femur. First tarsal segment plainly longer than second segment. Middle femur of male with long cilia on its ventral margin, and tibia also somewhat ciliate. No pegs present on femur. Hind femur of male with some short but inconspicuous cilia and a few larger hairs. Tibia with some longer scattered hairs. Metasternum about as long as first two ventral abdominal segments.

Abdominal venter with a moderate median longitudinal carina. Male genital segments shorter than the last two ventral pregenital abdominal segments. Rear margin of venter of the first genital of the male is characteristic of the species. It has two triangular projections. (See drawings on Plate 13, fig. 22d.) This character, combined with the ciliated middle legs and the general color pattern, readily identify the males of this species. The latter also identifies the females. The short black stripe on the base of the middle femur is characteristic of both sexes.

Comparative notes: A little smaller, on the average, than *L. cursitans* (Fabricius), has a black streak on the base of the middle femur that is lacking in all our specimens of *L. cursitans.* The latter lacks the triangular projections on the rear margin of the first genital male segment. Dr. Max Beier of Vienna kindly sent us a drawing of the male genital segments of the type from Java.

Data on distribution: This species was described from Java and reported by Kirkaldy from Fiji.

We have examined the following from:

Malay Peninsula: "Lenggong, Malay Peninsula Lea and Party." 1 male (S. Australian Museum).

Thailand (Siam): "Tong. Lower Siam. Dr. W. L. Abbott". 1 male (winged) (U. S. N. M.).

Sumatra: male and female (Kirkaldy Coll. K. U.).

Lesser Sunda Islds: "Sumbawa". 2 males (winged). (In our Kirkaldy coll.) These are 18 mm. long. One has width across humeri 3.15 mm., the other 2.77 mm.; one with width across the mesoacetabula 5.16 mm., the other 4.62 mm. "O Sumba, Langgai 13.7.1949 Dr. Bühler, Dr. Sutter". 1 male (Basel). "O Sumba Metoto, 4 Mai 1949. Dr. Bühler, Dr. Sutter. 1 male (Basel). "W. Sumba Kodi 3.8.1949. Dr. Bühler, Dr. Sutter. 1 female (Basel).

Borneo: "Borneo Multer" 1 female (Kirkaldy coll. K. U.); "Borneo, Schaner" 1 male (Bueno coll. K. U.); "Borneo, Samdahan, C. T. McNamera" 2 females (S. A. Mus.) via Hale.

Philippines: "Luzon, Manila 1913 Leg. G. Boetteker" 1 male, 1 female (winged) (British Mus.); "Luzon, 11-27-33. Victor Abalos" 1 female (winged); "Luzon, Manila Observatory Gardens" 7 females, 3 nymphs (Bueno coll. at K. U.); "Los Baños. P. I.—Baker" 3 males, 9 females (winged) (U. S. N. M. and K. U.).

Celebes: "Sumanga, S. Celebes Nov. 1895 H. Fruhstorfer" 1 female (winged). (In Kirkaldy coll. K. U.)

Moluccas: "Ternate 94 Kükenthal". 1 male, 1 female, winged. Male is 19 mm. long. (Bueno collection at K. U.); "Halmaheira, Soaknorra, Kükenthal". 1 male, winged, 17 mm. long. (In Kirkaldy coll. K. U.); "Dammer". 2 females (Kirk. coll. K. U.).

New Guinea: "N. Guinea, Bisiatabu, Port Moresby. W. N. Lock". 1 male. (S. Australian Museum).

New Britain: "Movenafen". 1 male, 1 female (winged) (Basel, Switzerland).

Solomon Islands: "Guadalcanal. 1944. L. J. Lipovsky". 8 males, 52 females (all winged); "Guadalcanal Jan. 1945. P. H. Eschmeier". 2 males, 3 females (all winged), the largest male 18.9 mm. long, while the largest female 14.2 mm. long. "Guadalcanal and Florida Is. I-III 1945 J. R. Stutz". 1 male (winged) is 17.25 mm. long. (Calif. Acad. Science); "Solomon Islands. July-Aug. 1909. W. W. Froggatt". 1 female (Bueno coll. K. U.).

Fiji Islands: "Viti Levu", 1 male, 1 female (both wingless) (In Kirkaldy coll. K. U.); "Viti Levu, Lami. 1-1951 Pool. N. L. H. Krauss". 3 females; "Coll. Camille, Van Volxem". 1 male (wingless). Det. as *G. ciliatus* (Mayr) by Kirkaldy 1898. This male is 15.33 mm. long. (In Kirkaldy coll. K. U.); "Viti Levu, Lami. 1-1951 Pool. N. L. H. Krauss". 3 females (winged); "Muanicula, Vanua Levu July 1934 P. W. Paine. In small shallow well." 2 males (winged); "Taveuni. Ura. Aug. 1934 P. W. Paine. Fresh water pool above high tide." 3 males, 5 females (wingless except one male); also "in shallow fresh water swamps above high tide". 3 females (wingless); "Taveuni. July 1934 P. W. Paine. Stagnant pool in rocky stream-bed in forest. 1000 ft." 1 female (winged) (the largest specimens taken by Paine are 15 mm. long); "Mvana, Vanua, Mbalavu VIII-938 Seashore. E. C. Zimmerman". 1 female (winged) (B. P. Bishop Mus.); "Bavatu, Vanna Mbalavu VIII-17-38 E. C. Zimmerman". 2 males (winged), 5 females (winged). (B. P. Bishop Mus.); "Wainiloka, Ovalan VII-11-38. Along stream. Elev. 200 ft. E. C. Zimmerman". 3 males, 8 females, 3 nymphs. (2 males and 5 females are winged.) (B. P. Bishop Mus.); "Matuku, 7-8-24. E. H. Bryan Jr." 1 male, 2 females; "Fieju" 1 male winged measuring 17.5 mm. in Uhler coll. (U. S. N. M.); "Rewa, Fiji. Muir 1906". 1 female (Bueno coll. K. U.).

Guam: "Merizo R. 10-19-45 D. G. Frey". 2 females, 3 nymphs, one female winged. (U. S. N. M.)

Limnometra inermis Mayr

(Pl. 3, fig. 15)

See under *Limnometra ciliata* Mayr for references. In the same paper and on the same page Mayr described *Limnometra ciliata* from Java. It was a large male 19.5 mm. long with cilia on middle femur. Then he described *Limnometra inermis* from Manila that he said was 13.6 mm. long and lacked the cilia on middle femur. He mistakenly thought it was a male. However, the type in Vienna is a female. It has the characteristic black streak on the base

of the middle femur that both sexes of *L. ciliata* have and is exactly like the females we have from the Philippines with which were taken the males of *L. ciliata.* The British Museum has a male and female taken in Manilla. The type lacks antennae and front legs entirely. The middle legs have only the femora which are 11.34 mm. long. The hind legs are gone. Actually the type measures 13.02 mm. long, 2.2 mm. across humeri and 3.46 mm. across middle acetabula.

Limnometra cursitans (Fabricius)

(Pl. 5, fig. 28; Pl. 14, fig. 23)

1794 *Gerris cursitans.* Fabricius, J. C. Ent. Syst. 4, 192 17. "Habitat in Nova Hollandia." (Old name for Australia.)
1803 *Hydrometra cursitans* Fabricius, J. C. Syst. Rhyn. p. 259.
1868 *Hydrometra cursitans* Stål, Carl Kongl. Svenska Vet. Akad. Handl. 7: 131-133. (Says belongs to *Limnometra* Mayr along with *L. fluviorum* Fabricius.)
1909 *Limnometra cursitans* Banks, C. S. Philadelphia Jour. Sci. 4 (6): 583.
1933 *Limnometra cursitans* Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4" p. 371. (Quotes Australia.)

This large Australian species measures from 15 to 22 mm. long and may reach 5.68 mm. across the middle acetabula. Like *L. ciliata* Mayr the males have the middle femora abundantly supplied with long cilia as are the tibiae. The hind femora and tibiae are also ciliated. The middle and hind femora are longer than the body. The front femora stouter. The first tarsal segment plainly longer than the second. The rear margin of the venter of the first genital segment of the male is slightly produced laterally.

Location of type: The type is in the British Museum.

Data on distribution: We have before us the following:

Australia: "Australia, Pr. of Wales Isl. II-15-1939, R. G. Wind." 12 males, 14 females, all winged. (K. U. col.).

New Guinea: "Merauke, Dutch New Guinea. III-27-1939. R. G. Wind." 7 winged (3 males, 4 females); 11 wingless (2 males, 9 females).

Limnometra femorata Mayr

(Pl. 5, fig. 27; Pl. 13, fig. 21)

1865 *Limnometra femorata* Mayr, Gustav L. Verh. Zool-bot. Vereins, Wien 15: 443.
1865 *Limnometra femorata* Mayr, Gustav L. Hemiptera in Novara Expedition Zool. Theil. Wien, 2 (1): 174. (Places in his key to species.)
1909 *Limnometra femorata* Banks, C. S. Philippine Jour. Sci., 4 (6): 582.
1931 *Limnometra femorata* Esaki, T. Bull. Biogeographical Soc. Japan, 9 (2): 211.
1933 *Limnometra femoratus* Lundblad, O. Archiv für Hydrobiologie. Suppl. 12 "Tropische Binnengewässer 4," p. 371. (Lists Borneo and Philippines.)
Also referring to the above species:

1901 *Gerris* (*Limnometra*) *kirkaldyi* Breddin, G. Rev. Ent. 20: 93. (Described from "Ins. Banguey prope Borneo.) In Breddin's collection.
1905 *Gerris kirkaldyi* Breddin, G. Mitt. Naturhist. Mus. 22: 214 (records).
1933 *Limnometra kirkaldyi* Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4," p. 371.

Mayr described this large gerrid from the Philippines. The following brief description will identify it.

Size: 15-23 mm. long. The males usually larger than the females.

Color: General color light brown with the usual black stripes. Hemelytra brown. Last antennal segment white. Middle and hind femora pale near tip. Distal half of middle tibia pale.

Structural characters: Proportional length of antennal segments: 1st: 2nd: 3rd: 4th:: 200: 145: 206: 208. Total length of antenna 15.94 mm. Length of insect 23 mm. Middle femur of male longer than the body. Front femur slender, not thicker than middle femur, its first tarsal segment a little longer than second. The males with a large, somewhat curved spine near distal end of middle femur and two rows of about fifteen pegs. Connexival spines long and slender.

Location of type: In the Natural History Museum in Vienna.

Comparative notes: The large spine near the distal end of the middle femur of the male is characteristic of this species and of *L. kirkaldyi* Breddin. The former was described from the Philippines and the latter from the Island of Banguay, north of Borneo and south of Balbaboe Island of the Philippines. We have a male from Banguey that was labeled by Breddin "Gerris kirkaldyi Bredd," and eight other specimens from Banguey that also probably came from Breddin and are in the Kirkaldyi collection at the University of Kansas. All of these are the same color as the Philippine specimens with only a trace of pink on the pronotum and with light brown hemelytra and clear, slightly darker veins. Since they are also structurally the same as *L. femorata* Mayr, we must record *Gerris kirkaldyi* Breddin as a synonym. However, all the specimens we have seen from Borneo are beautiful specimens with light reddish pronotum and bluish-black hemelytra with black veins. They would have been more deserving of a name than *L. kirkaldyi* (Breddin) which has nothing to distinguish it from *L. femorata* Mayr.

Data on distribution:

The Philippines: "Island Samar, Baker." 4 males (U. S. N. M.); "Island Sibuyan, Baker." 1 male (U. S. N. M.); "Iligan, Mindanao,

Baker." 2 males, 1 female (U. S. N. M.); "Zamboanga, Mindanao, Baker." 1 male (U. S. N. M.); "Davao, Mindanao, Baker." 1 female (U. S. N. M.); "C. N. H. M. Philippine Zool. Exp. (1946-47) F. G. Werner Leg. E. Slope Mt. McKinley, Davao Province, Mindanao, stream through original forest." 1 male (Chicago, N. H. M.); "C. N. H. M. Philippine Zool. Exp. (1946-47) VIII, 22, 1946 H. Hoogstraal. E. Slope Mt. McKinley, Davao Prov., Mindanao. Forest stream." 1 female (C. N. H. M.); "Surigao, Mindanao." 1 male (British Mus.); "Philippine Islands, Basilan, Maloong. vend. M. E. Walsh." 1 male (British Mus.).

Banguey Island: "Banguey, Borneo." 1 male labeled by Breddin "*Gerris kirkaldyi* Bredd." and may be the type. (Kirkaldy coll. K. U.); "Banguey Ins. nordl. Borneo. W. Kedengurg det. 20, VII, 1894." 1 male, 6 females. (Kirkaldy coll. K. U.); "Banguey." 1 male labeled *femorata* but not by Breddin.

Borneo: "Nord. Borneo ex. col. Fruhstorfer." 1 female (Kirkaldy coll.); "N. Borneo. Kenabatangan Dist. S. E. end of Dewhurst Bay. C. N. H. M. Borneo Zool. Exp. 1950. R. F. Inger and D. D. Davis leg." 1 male, 1 female (C. N. H. M.); "O. Borneo. Dagavenan, Sangkoelirang Dist. M. E. Walsh." 1 male, 1 female (Basel, Switzerland); "Muller, Borneo." 1 male (Kirkaldy coll. K. U.); "Kuching." (Beebe) 1 male, 1 female.

All of the Borneo specimens have a reddish pronotum and blue-black hemelytra with black veins.

Limnometra nigripennis Mayr

(Pl. 4, fig. 26; Pl. 14, fig. 24)

1865 *Limnometra nigripennis* Mayr, Gustav L. Verh. zool-bot. Vereins, Wien, 15: 443.
1865 *Limnometra nigripennis* Mayr, Gustav L. Hemiptera in Novara Expedition Zool Theil, Wien, 2 (1): 174. (Places in key to species.)
1933 *Limnometra nigripennis* Lundblad, O. Archiv. für Hydrobiologie Suppl. 12 "Tropische Binnengewässer 4", p. 371.

Mayr described this species as follows:

"*L. nigripennis* n. sp. Long. 14 mm. Laete fulva, pronoto nigrolineato, capite supra lineis 2 longitudinalibus antice confluentibus, fuscis, mesosterno utrinque ad pronoti marginem linea angusta nigra, tegminis cinereo-nigris margine externe laete flavo, acetabulis pedum intermediorum muticis, pedibus fulvis aut brunneis, femoribus intermediis non ciliatis, aute apicem seriebus 2 spinularum minutissimarum sine spina longa, femoribus posticus apice flavis, tibiis tarsisque pedum posteriorum nigricantibus. Philippinen."

The type is a winged male 13.44 mm. long, 2.1 mm. across the head, 2.31 mm. across humeri, 3.53 mm. across mesoacetabula. Its abdomen is somewhat dermestid-eaten beneath. One antenna lacks the last two segments. The right front leg and right middle leg are gone. The right hind leg has lost its tarsus and the left hind leg has only one, the femur. The left middle leg has lost its last tarsal segment. The left middle femur has some short cilia on the margin of the distal one fourth and two rows of pegs, seven pegs in one row and eight in the other, the tibia has a fringe of short cilia throughout its entire length and a row of short, black procumbent spines paralleling it. The antennal formula is, 1st: 2nd: 3rd: 4th:: 145: 103: 130: 95?*. The fourth segment is white. The second antennal segment is equal to head width.

This species is quite variable in color and relative length of antennal segments. Typically, the winged forms have the costal margin of the hemelytra strikingly lighter than the remainder of the wing but there are specimens that do not show this. Typically the second and third antennal segments have a pale or even white band and the distal segment is white, except its base. All have the last antennal segment white. The antennae are long and slender, as long as the body. In the type and some other specimens the second antennal segment is not longer than the width of the head but in many it is considerably longer and in some specimens the second segment may be equal to head width in one antenna and longer in the other. Front leg with first tarsal segment a little longer than second one. The mesosternum may be bare or partially covered with short cilia. In apterous forms typically the abdominal tergites are dark with a more or less apparent median longitudinal lighter stripe on last four or five segments and connexivum pale. However, there are some specimens that do not have the striking pattern described above.

We have a series of "Island Samar-Baker" 5 males (2 winged), 3 females (apterous) (U. S. N. M. and K. U.). The winged forms have the pale costal margin; wingless forms have black abdominal tergites with paler median stripes on the last 4 or 5, and a pale connexivum. Both sexes have the fringe of short cilia and parallel row of procumbent spines on middle tibia. The middle femur of male may have a band of very short cilia on its rear margin.

* Last segment may be broken.

The relative length of antennal segments:

	1st:	2nd:	3rd:	4th::	2nd seg.: head width::
w. ♂	160:	110:	185:	175	5.6: 4.7
w. ♂	165:	120:	185:	?	5.8: 4.75
a. ♂	177:	138:	210:		6.8: 4.95
a. ♂	210:	142:	215:	?	10.5: 5.35
a. ♂	190:	144:	220:	201	7.2: 5.1
					L. 5.3: 4.7
a. ♀	R. 142:	94:	142:	130?	R. 4.7:
a. ♀	132:	102:	155:	130	5.1: 4.7
					4.6: 4.6
a. ♀	140:	92:	145:	170	4.65

W. = winged; a. = apterous; R. = right; L. = left.

Data on distribution:

"Baguio. P. I. W. Robinson". 1 female winged with pale costa and banded antennae, 2nd antennal segment slightly longer than head width.

"Los Banos, P. I. Baker". 3 males (winged), 3 females (wingless) (U. S. N. M. and K. U.). antennae more or less banded, last segment white. 2nd antennal segment from less than to considerably more than head width. The winged male with narrow pale costal margins. The apterous with abdominal tergites dark, with more or less paler longitudinal median stripes on last four or five abdominal segments. Connexivum yellow.

Philippines: "Island Polillo, Baker". 1 male, 1 female, apterous. (U. S. N. M.); "Kolambugan, Mindanao Baker". 1 winged female. Costal margin *not* pale. 3rd antennal segment ringed. (U. S. N. M.); "Laguna, Mt. Maquiling, Luzon. P. I. 5,28-30 A. Durjag." 1 male, wingless. (U. S. N. M.); "Majayjay, Laguna, Luzon. P. I. R. C. M. C. Gregor." 1 male, 1 female, apterous. (U. S. N. M.); "Guintaboan, Victorias. Occe. Negros." 1 male (U. S. N.M.); "Guimaras P. I." 1 female; "Calian, Davao Prov., Mindanao. Phil. Islds. C. S. Clagg 31, V." 2 males, 2 females. (M. C. Z.); "Philippines." 3 males apterous. (Kirk. coll. K. U.); "Palawan Is. 750 ft. V-2-47 F. G. Werner" 2 males (winged) (C. N. H. M.); "Busuanga Is. P. I. H. Hoogstraal". 1 female (winged) (C. N. H. M.); "Busuanga Is. P. I. H. Hoogstraal". 2 males (winged), 2 females (apterous) (C. N. H. M.); "Davao Prov., Mindanao sea level. 47 H. Hoogstraal". 1 male, 1 female (apterous); "Mindanao 1500 ft. 47. F. G. Werner". 3 males (apterous), 9 females (1 winged) (C. N. H. M.); "Davao, Mindanao Baker". 3 females (winged), last ant.

seg. white. (U. S. D. A.); "Zamboanga, Mindanao Baker". 4 females (winged), last ant. seg. white, 2nd = head width. (U. S. N. M.); "Davao, Mindanao. R. C. McGregor". 2 females (winged) (U. S. N. M.).

In the last three lots above all have only last ant. seg. white, and 2nd seg. short and costal margin of wings not paler.

"Luzon. P. I." 1 male, 2 females (apterous), antennae banded. Connexivum pale. (Kirk. coll. K. U.); "Luzon". 1 male, 1 female (apterous) (Bueno coll. K. U.).

Limnometra pulchra Mayr

(Pl. 4, fig. 23; Pl. 15, fig. 25)

1865 *Limnometra pulchra Mayr*, Gustav L. Verh. Zool-bot. Vereins, Wien, 15: 443-444. "Java".
1865 *Limnometra pulchra* Mayr, Gustav L. Hemiptera in Novara Expedition, Zool. Theil, Wien, 2 (1): 174. (Places in a key with six other species.)
1901 *Gerris pulchra* Breddin, Gustav. Abh. Nat. Ges. Halle, 24: 20, 85. (Quotes "Celebes. [S. Walk., He. VIII p. 168]—Jave, Borneo.")
1901 *Gerris pulchra* Kirkaldy, G. W. Ann. Mus. Civ. Stor. Nat., Genova 20 (2): 804 (These are from New Guinea and are not *Limnometra pulchra* Mayr but *Limnometra kallisto* Kirkaldy.)
1903 *Gerris pulchra* Breddin, Gustav. Abh. Senck Nat. Ges., 25: 164. (Lists Halmahera (Oba 232).
1920 *Limnometra pulchra* Horváth, G. Abh. Senck. Nat. Ges., 35: 313. (Gives distribution as: Java, Borneo, Celebes, Amboina and New Guinea. New for Aru Island.)
1933 *Limnometra pulcher* Lundblad, O. Archiv. für Hydrobiologie 1933. Suppl. 12. "Tropische Binnengewässer 4", p. 371. (Lists: Java, Aru-Inseln, Borneo?, Celebes, New Guinea, Molukken.)

Size: Mayr gives 14.5-16 mm. long. However, we have specimens ranging from 12-17 mm. long. The males are larger than the females.

Color: A tan colored species. A faint figure M on the head with only the margins next the eyes showing dark brown to black. The usual median longitudinal black line, bordered by pale lines on pronotum. Lateral black lines extending from front margin to the base of humeri. Behind the humeri a dark line parallels the margin which is pale yellowish in color. This yellow stripe lying laterad of the black stripe is continued forward on either side of eye. There is a black stripe on the side of prothorax and another one on the proacetabulum. An undulating band on mesopleuron ends above the mesocoxa. Another black band on mesoacetabulum and two on metaacetabulum. Abdominal tergites reddish. Antennae uniformly brown. The ends of middle and hind femora pale.

Structural characteristics: The antennal formula for the male type: 1st: 2nd: 3rd: 4th:: 160: 125: 140: 170. The first tarsal

segment of the front leg is plainly longer than the second. All males have mesosternum densely covered with long whitish hairs and all three femora are fringed with cilia, that of the hind femur shorter but plainly visible. The middle femur of the male with many little black pegs among the cilia and two rows of eight or more pegs near distal end. The connexival spines of the female are relatively shorter than in the male. The middle and hind femora as long as the body in the male, a little shorter in female.

Location of types: In the "Zoologische Abteilung des Naturhistorischen Museums in Wien." Four male specimens in Mayr's type series. The male bearing his own label "*pulchra*" and "Dr. Doleschal 1859, Amboina" may be designated the type. There are two other males with the same locality and collector label. A fourth male labeled "Molukken. Coll. Signoret." These specimens fit his brief description but do not come from "Java" as he records in his description. However, Dr. Beier assures us that these are the types. They came from the Moluccas.

Comparative notes: Dr. Mayr 1869, published a key to seven species of *Limnometra* including *pulchra* which is useful. There are three very close and often confused species. *L. pulchra,* in which the males have both the middle and hind femora plainly fringed with cilia and *L. annulicornis* (Breddin) and *L. kallisto* Kirkaldy that have only the middle femora fringed with cilia and have the connexival spines a little longer, especially in the females.

Data on distribution: Moluccas: "Amboina, Dr. Doleschal 1859" 3 males comprising the type series and 1 male labeled "Molukken. coll. Signoret"; "Amboina v. 1909 coll. F. Muir" 1 male, 1 female. (K. U.) and several in (H. S. P. A.); "Prov. Ceram. F. Muir, Jan. 1909" 3 males, Febr. 1909, 1 male (Calif. Acad. Sci.); "Forsten, Ceram" 3 males, 1 female (Kirk. coll. K. U.); "Buru" 1 male (Bueno coll. K. U.)

Java: "Java occident. Mons Gede, 4000 Aug. 1892. F. Fruhstorfer." 1 male, 2 females. (Vienna); in the Bueno collection as part of the type series of *G. annulicornie* Breddin we find a female with the label just above and Breddin's label "*Gerris* n. spec. nicht *pulchra*." But it is *pulchra*.

Celebes: Here belong two more specimens from Breddin's type series of *G. annulicornis*, namely "Halmaheira Soa komorra, Kükenthal" "*Gerris annulicornis* Bredd." female and "Halmaheira, Oba 94, Kükenthal" a male typical of *L. pulchra* Mayr.

Limnometra pulchra tanganyikensis subsp. nov.

(Pl. 4, fig. 25)

Three specimens labeled "Tanganyika S." in the Kirkaldy collection in the University of Kansas collection are the only true *Limnometra* that we have seen from Africa. There is one male that has lost its abdomen and two females, none of them has the antennae present. The color pattern is the same as in *L. pulchra* Mayr and the male has all three femora fringed with cilia and the mesosternum hairy as in *L. pulchra*. We are therefore making it a subspecies of *Limnometra pulchra* Mayr in spite of its distance from the present distribution of *L. pulchra* as we know it.

Size: Winged male: 12.7 mm. long; width across humeri 2.06 mm.; width across mesoacetabula 2.98 mm.; width across head 1.93 mm.; winged female: 12.2 mm. long; width across mesoacetabula 3.05 mm.; width across head 1.85 mm.

Color: Color and pattern as in *L. pulchra* Mayr. See illustrations on Plate 4, figures 23 and 25.

Structural characteristics: Antennae are gone. Front femur of the male plainly stouter than middle femur and fringed beneath with cilia; first tarsal segment plainly longer than the second. Middle and hind femora fringed with cilia, that of hind femur shorter but plainly visible. The middle femur of the male with many little black pegs among the cilia. The connexival spines of the female are relatively shorter than in the male. Middle femur not quite as long as the body in the male and shorter in the female.

Location of types: Described from one male and two females from Tanganyika in the Kirkaldy collection of the Francis Huntington Snow Entomological Museum, University of Kansas.

We would like to see other specimens of *Limnometra* that are taken in Africa.

Limnometra annulicornis Breddin

(Pl. 4, fig. 24; Pl. 15, fig. 26)

1901 *Gerris annulicornis* Breddin, Gustav. Abh. Nat. Ges., Halle, 24: 20, 83-85. (Describes from Celebes.)

1933 *Limnometra annulicornis* Lundblad, O. Archiv für Hydrobiologie. Suppl. 12. "Tropische Binnengewässer 4," p. 371. (Quotes Celebes.)

Evidently, this species has not been seen since it was described over fifty years ago. We have found in the Kirkaldy collection here at the University of Kansas what appears to be Breddin's type series. The labels are in Breddin's handwriting. There are six

specimens. Three labeled "Celebes Sar. Kratertümpel des Masarang" (one male labeled *Gerris annulicornis* Bredd. and two females). These fit his description and have the second antennal segment annulated. They are undoubtedly of his species. The other three are *L. pulchra* Mayr: a female from "Halmaheira Soa konorra. Kükenthal" labeled by Breddin *Gerris annulicornis* Bredd., a male from "Halmaheira, Oha, 94. Kükenthal" with the following label in Breddin's handwriting: "*Gerris olim pulchra* Bredd. (Kükenthal Hem. p. 164) nicht die Mayr sp." and a female labeled "Java occident. Mons Gede 4000' Aug. 1892 H. Fruhstorfer" labeled by Breddin "*Gerris* n. spec. (*nicht pulchra.*). However, it is *L. pulchra* Mayr and there is one male and two females with the same locality label in the Vienna Museum.

We have then only three specimens of *L. annulicornis* (Breddin): One male, which we consider the type and two females. We supply the following information from these specimens.

Size: The male type is 15 mm. long; 3.27 mm. across mesoacetabula; 1.89 mm. across head. The females a little smaller.

Color: About the same as *L. pulchra* but a little darker. The figure M on the head is very distinct and the lateral dark bands on the anterior lobe of pronotum are broader. These lateral bands are continuous beneath the humeri in this species but broken in *L. pulchra.* The second antennal segment has a pale annulation on its distal half.

Structural characteristics: The proportional length of antennal segments of male type: 1st: 2nd: 3rd: 4th:: 130: 80: 115: 130. Total length of antenna about 9.56 mm.; the second segment shorter than width of head across the eyes. Front femur plainly stouter than middle femur; the first and second tarsal segments of the front leg subequal. The fringe of cilia on middle femur of male about as long as the diameter of the femur. Only four small pegs in a single row near distal end of femur. The hind femur without a fringe of cilia. The mesosternum not exactly bare but not hairy as in *L. pulchra.* The middle and hind femora not as long as the body. Connexival spines rather long in both sexes.

Location of types: One male and two females bearing the label "Celebes Sar. Kratertümpel des Masarang" in the Kirkaldy collection at the University of Kansas.

Comparative notes: This species was confused with *L. pulchra* Mayr by Breddin but the males may be easily separated from that

species because the hind femur of the male is not fringed with cilia and its second antennal segment is shorter than the width of the head. The connexival spines of female are longer and the second antennal segment is annulated.

Distribution: Known only from the types from Celebes.

Limnometra vulpina (Breddin)

1901 *Gerris vulpina* Breddin, Gustav. Abh. Nat. Ges., Halle, 24: 20, 85-85.
1933 *Limnometra vulpina* (Breddin) Lundblad, O. Archiv für Hydrobiologie Suppl. 12. "Tropische Binnengewässer 4," p. 371. (Quotes Celebes.)

Dr. Breddin described this species from a single female from North Celebes "(Matinang-Kette, Sudseite, 800-1200 m. (Sar.))" and gave its size as 15½ mm. long and 4 mm. across the middle coxae. We cannot locate this type. He stated that it had longer connexival spines than his *Gerris annulicornis*. However, since Dr. Breddin identified specimens of *L. pulchra* Mayr as his *G. annulicornis* and the females of *L. pulchra* have shorter connexival spines, he probably compared his female *G. vulpina* with a female of *L. pulchra* Mayr and said its connexival spines were longer than in *G. annulicornis* when his *L. vulpina* was really a very large pale *G. annulicornis*. Until both males and females from North Celebes make this species recognizable we will consider it a synonym of *G. annulicornis*.

Limnometra kallisto (Kirkaldy)

(Pl. 5, fig. 31; Pl. 16, fig. 27)

1899 *Gerris kallisto* Kirkaldy, G. W. Ann. Soc. Ent. Belg., 43: 506. (Desc. female from Mysol. [W.] which is west of New Guinea.)
1899 *Gerris kallisto* Kirkaldy, G. W. Ann. Mus. Civ. Stor. Nat., Genova, ser. 2.a, 20 (40): 804. (Reports female from "New Guinea, Dorei Hum, Jan. 1875 Beccari".)
1933 *Limnometra kallisto* (Kirkaldy) Lundblad, O. Archiv für Hydrobiologie. Suppl. 12. "Tropische Binnengewässer 4", p. 371. (No additions.)

Kirkaldy described this species from a single female. He says: "Belongs to subgenus *Limnometra* Mayr. ♀. First antennal segment one-third longer than the second, one-twelfth longer than the third, fourth twice as long as the second. Apex of rostrum reaching to two-fifths of the length of the mesosternum, which is narrowly canaliculate for half its length. Base of pronotum subacutely triangular. Mesosternum feebly tuberculate. First segment of anterior tarsi one-half longer than the second. Sixth segment of abdomen feebly emarginate beneath, a little swollen apically, connexival spines prolonged scarcely beyond the apex of the abdomen. Elytra scarcely reaching the apex of the abdomen. Length 11.7

mm.; width 2.4 mm. Mysol (W.) Higgins 1869 coll. Van Volxem. Cinnamon; head immaculate, first and second antennal segments pale yellow, third and fourth darker. Pronotum with a central and two lateral narrow and blackish lines, the former margined with pale yellow on each side, reaching to the base of the pronotum, the latter reaching to the base of the median lobe of the pronotum; posterior lobe margined with pale yellow (a little reflexed), submargined with brownish. Elytra with darker nervures. Apex of intermediate and posterior femora, apical half of intermediate and posterior tibiae, and all the tarsi entirely (black apical segment of anterior tarsi excepted) pale yellow. Venter obscure yellow."

Dr. A. Collart has informed us that this species is no longer to be found in the Royal Museum of Belgium. In 1928 the senior author saw in that museum the type of *Velia albotrimaculata* Kirkaldy which was described in the same paper. What has become of the female type of *Gerris kallisto* Kirkaldy is a mystery.

We found, however, in the Kirkaldy collection a female labeled "*Gerris kallisto* Kirk." by Kirkaldy and bearing the label "N. Guinea Dorei Hum. II Beccari 1875". The month does not agree with the one reported in his second paper but it is undoubtedly the same specimen and in the absence of the type from Mysol we are submitting drawings of this specimen and some descriptive notes, but must point out that while it does not meet the specifications of the description of *Gerris kallisto*, unfortunately neither do some of Kirkaldy's known types of other species fit the published descriptions. Moreover, we find in the Kirkaldy collection specimens he had labeled as *G. pulchra* (Mayr) yet the females are structurally indistinguishable from the female he had labeled *G. kallisto*.

We find this species to vary in size from 11.7 mm. to 20 mm. long. The males have the middle femur with a row of short cilia less than one-half as long as diameter of the femur and the hind femur without cilia. The middle femur may or may not have pegs and seems to be a variable character in this species. The first tarsal segment of the front leg is plainly longer than the second.

Distribution:

Moluccas: "Mysol (W.) Higgins 1869 Coll. Van Volxem" the female type.

New Guinea: "N. Guinea Dorei Hum II Beccari 1875. A female labeled by Kirkaldy *Gerris kallisto* Kirk. (Kirk. coll. K. U.); "N. Guinea, Dilo Loria VI, VII, 90." 1 male, 2 females (Kirk. coll.

K. U.); "N. Guinea, S. E. Haveri, Loria VII-XI, 93" 2 males, 4 females (Kirk. coll. K. U.); "Laloki, Papua" 1 male. (Kirk. coll. K. U.); "N. Guinea, R. S. Roberts Siph. 1944." 1 male, 1 female; "N. Guinea Milne B." 1 male (Bueno coll. K. U.); "N. Guinea S. E. Maroka 1300 m. Loria VII-XI. 93" 2 large males, 20 mm. long. (Labeled by Kirkaldy *Gerris pulchra* Mayr.); "Maffin Bay, Dutch N. Guinea. VI-II-44. E. S. Ross" 2 males, 1 female (Calif. Acad. Sci.); "Finschhafen, New Guinea, IV-15-44. E. S. Ross" 1 female. Another female IV-21-44. (Calif. Acad. Sci.); "Wareo, Finsch Haven, New Guinea, Rev. L. Wagner" 3 males, 3 females. (South Australian Mus.); "Brena Bay, N. E. Papua, C. T. M. C. Namara" 1 female (South Australian Mus.); "Mt. Lamongton, N. E. Papua. 1300-1500 ft. C. T. McNamera" 3 males, 3 females. (South Australian Mus.); "Mt. Gyifrie, N. New Guinea, sea level 1000 ft. April 39 L. E. Cheeseman" 10 males, 7 females. The males having long front femora, not stouter than middle femora and second antennal segment longer than head width.

With the same label we find 3 males that have stout front femora, second antennal segment not longer than broad width and middle femora with many black pegs among the cilia. Seems to be a variant of the above.

New Britain: "Movehafen" 1 male (Basel Mus.).

Solomon Islands: "Solomon Is. July-Aug. 1900 W. W. Froggatt" 1 male (Bueno coll. K. U.); "Guadalcanal XI-21-1944. L. J. Lipovsky" 2 males, 3 females. (K. U.); "Solomon Is. T. H. L. Waterhouse" 2 males, 1 female (South Australian Mus.).

PLATE I

FIG. 1. *Tenagogonus albovittatus* Stal
- a. Winged female. Gabon
- b. Antennae of the winged female. Gabon
- c. Wingless male. Sangmelina Cameroons, West Africa, Dec. 17, 1934, A. I. Good

FIG. 2. *Tenagogonus zambezinus* (Poisson)
- a. Wingless male. S. Rhodesia, S. Africa, G. E. Hutchinson
- b. Wingless female. Nagapa Res. Lab. Zululand, Africa, Apr. 22, 1922, H. H. Curson

FIG. 3. *Tenagogonus madagascariensis* Hoberlandt
- a. Wingless male. Environ de Rogez, Madagascar (paratype)
- b. Wingless female. The same data as above.

FIG. 4. *Tenagogonus divergens* Hungerford and Matsuda
- a. Brook near Bawomataluwo, Sumatra. Sept. 12, 1931, v. d. Meer Mohr (holotype)

FIG. 5. *Tenagogonus kampaspe* (Kirkaldy)
- a. Wingless female. Rigo, New Guinea. July, 1889, L. Loria (type series)
- b. Winged male. Kelsei, New Guinea. Nov.-Dec. 1890, L. Loria (type series)
- c. Wingless male. Rigo, New Guinea. July, 1889, L. Loria (type series)

FIG. 6. *Tenagogonus robustus* Hungerford and Matsuda
- a. Wingless female. Lavang, East Java. (type series)
- b. Brachypterous male. Pogobina, West Sumba. Sept. 17, 1949, D. Bühler, Dr. Sutter (type series)

PLATE I

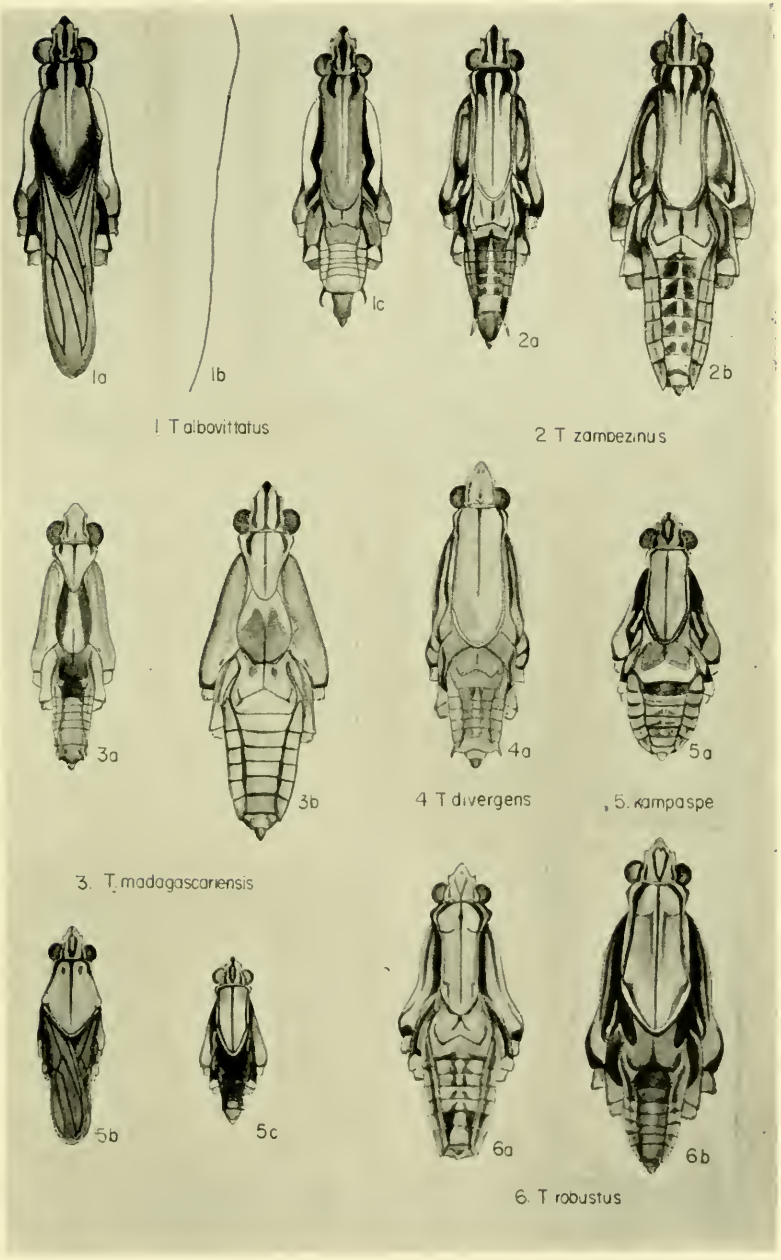

1a
1b
1c
1 T albovittatus
2a
2b
2 T zambezinus
3a
3b
3. T. madagascariensis
4a
4 T divergens
5a
5. kampaspe
5b
5c
6a
6b
6. T robustus

PLATE II

FIG. 7. *Tenagogonus robustus claggi* Hungerford and Matsuda
- a. Wingless female. Mt. Apo, Mindanao, Philippine Islands. C. F. Clagg (type)

FIG. 8. *Tenagogonus brevis* (Lundblad)
- a. Winged (copied from Lundblad)
- b. Wingless female. Java. Thienemann (allotype)

FIG. 9. *Tenagogonus fijiensis* Hungerford and Matsuda
- a. Wingless male. Taveuni, Fiji Island. July 1934. R. W. Paine (type series)

FIG. 10. *Tenagogonus pravipes bergrothi* Hungerford and Matsuda
- a. Wingless female. Observatory Garden, Manila, Philippine Islands (type series)
- b. Winged male. The same data as above.

FIG. 11. *Tenagogonus kuiterti* Hungerford and Matsuda
- a. Wingless male. Mohnyin, Burma. Oct. 27, 1944. K. C. Kuitert (type series)
- b. Winged male. The same data as above.
- c. Antenna of winged male. The same data as above.
- d. Winged male. The same data as above.
- e. Wingless male. The same data as above.

FIG. 12. *Limnometra borneensis* Hungerford and Matsuda
- a. Winged male. Tandjong Morawa, Serdang, N. E. Sumatra. Dr. B. Hagen (type series)

FIG. 13. *Limnometra minuta* Mayr
- a. Antenna. Novara Expedition, Sambelong. (type)
- b. Winged male. The same data as above.

PLATE II

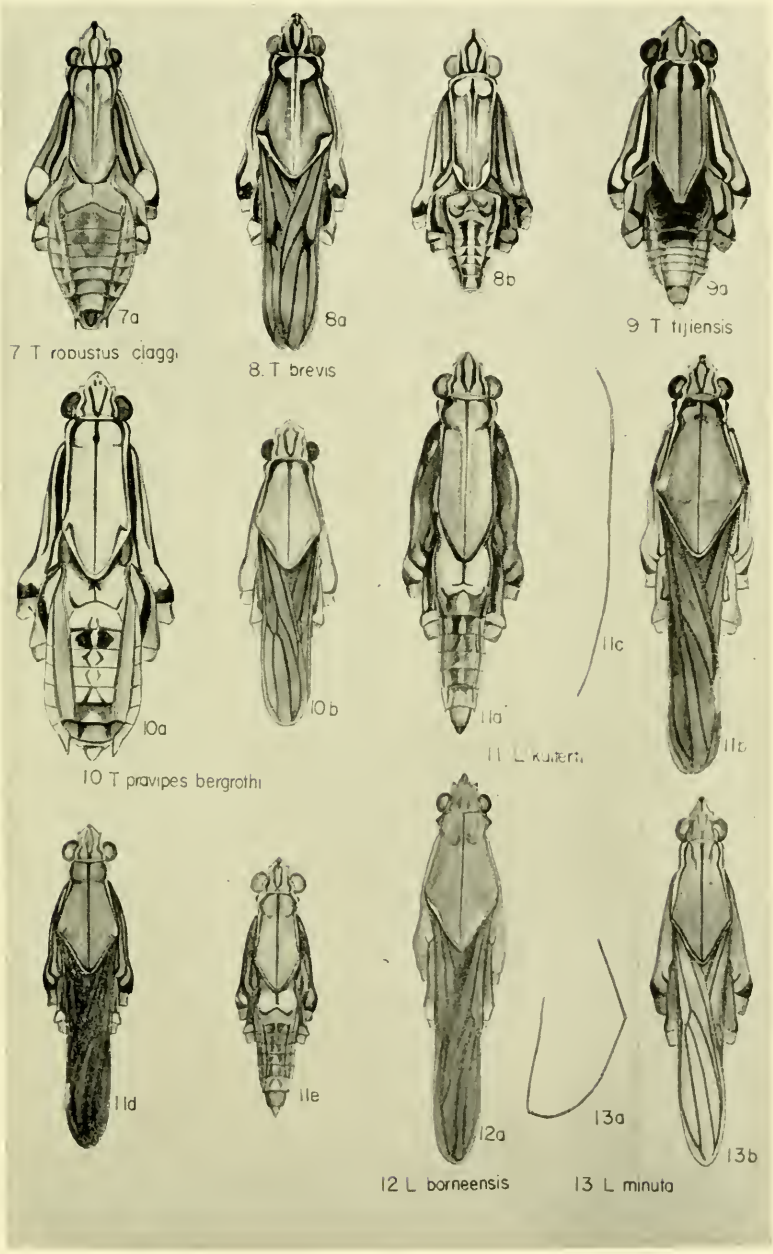

7a
8a
8b
9a
7 T robustus claggi
8. T brevis
9 T fijiensis
10a
10b
11a
11c
11b
10 T pravipes bergrothi
11 L kuiteri
11d
11e
12a
13a
13b
12 L borneensis
13 L minuta

PLATE III

FIG. 14. *Limnometra ciliata* Mayr
- a. Winged male. Sumbawa, Lesser Sunda Islands
- b. Winged female. Rewa, Fiji. 1903, Muir. Showing an individual with black pronotum.

FIG. 15. *Limnometra inermis* Mayr
- a. Winged female. Novara Expedition, Manila (type)

FIG. 16. *Limnometra palauana* Esaki
- a. Winged female. Toloas, Truk, Caroline Islands. Jan. 21, 1938, T. Esaki (type series?)
- b. Front leg. The same data as above.

FIG. 17. *Limnometra palauana* Esaki?
- a. Winged male. Los Negros, Admiralty Island

FIG. 18. *Limnometra rossi* Hungerford and Matsuda
- a. Winged female. Mindoro, Philippine Islands. Jan. 28, 1945, E. S. Ross (type series)

FIG. 19. *Limnometra fluviorum* (Fabr.)
- a. Winged male. Tanjore Dist. Nedungadu, India. Mar. 12, 1938, P. Susai Nathan

FIG. 20. *Limnometra lipovskyi* Hungerford and Matsuda
- a. Winged male. Guadalcanal. 1944, L. T. Lipovsky (type series)

PLATE III

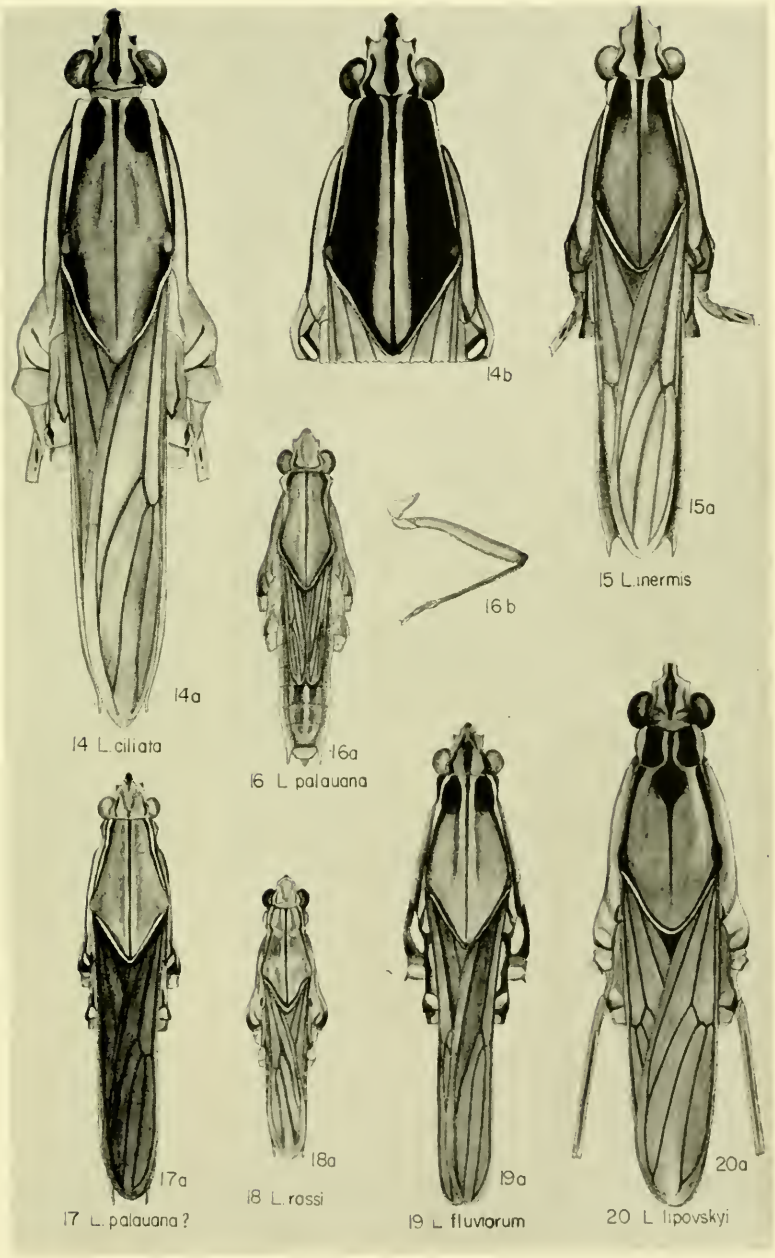

14a
14 L. ciliata
14b
15a
15 L. inermis
16b
16a
16 L. palauana
17a
17 L. palauana?
18a
18 L. rossi
19a
19 L. fluviorum
20a
20 L. lipovskyi

PLATE IV

FIG. 21. *Limnometra insularis* Hungerford and Matsuda
- a. Winged male. Tandjong Morawa, Serdang, N. O. Sumatra. Dr. B. Hagen (holotype)
- b. Antenna of winged male. The same data as above.

FIG. 22. *Limnometra octopunctata* Hungerford
- a. Wingless female. Tandjong Morawa, Serdang, N. O. Sumatra. Dr. B. Hagen (allotype)
- b. Wingless male. The same data as above. (holotype)
- c. Wingless male. The same data as above. (holotype). Ventral side.

FIG. 23. *Limnometra pulchra* Mayr
- a. Amboina. May, 1909, E. Muir (type)

FIG. 24. *Limnometra annulicornis* Breddin
- a. Winged female. Kratet Tümpel der Mararang, Celebes. Breddin (type series)

FIG. 25. *Limnometra pulchra tanganyikensis* Hungerford and Matsuda
- a. Winged male. Tanganyika (type)

FIG. 26. *Limnometra nigripennis* Mayr
- a. Winged male. Samar Island. Baker

PLATE IV

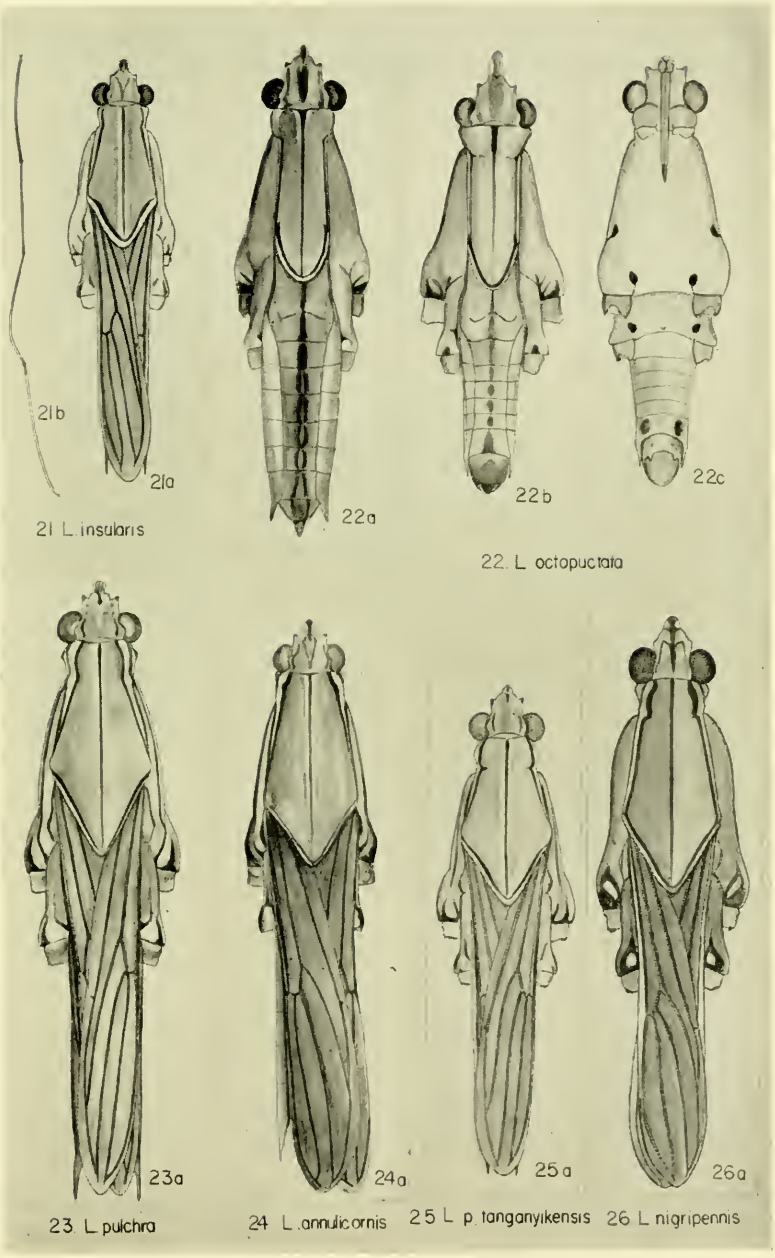

21b
21a
22a
22b
22c
21. L. insularis
22. L. octopuctata
23a
24a
25a
26a
23. L. pulchra
24. L. annulicornis
25. L. p. tanganyikensis
26. L. nigripennis

PLATE V

FIG. 27. *Limnometra femorata* Mayr
- a. Winged female. E. slope, Mt. McKinley, Davao prov., Mindanao, Philippine Islands. 1946-47, F. G. Werner
- b. Middle femur of female. The same data as above.

FIG. 28. *Limnometra cursitans*
- a. Wingless female. Merauke, Dutch New Guinea. Mar. 27, 1939, K. G. Wind

FIG. 29. *Tenagogonus grandiusculus* Poisson
- a. Wingless female. Sangmelina, Cameroon, W. Africa. Apr. 16, 1932, A. I. Good (Determined by Poisson)
- b. Antenna of wingless female. The same data as above.

FIG. 30. *Limnometra anadyomene* (Kirkaldy)
- a. Wingless male. Suduganga River, Matale, Ceylon. R. A. Senior-White (type series)
- b. Wingless female. Punduloya, Ceylon. E. E. Green (type series)

FIG. 31. *Limnometra kallisto* (Kirkaldy)
- a. Winged male. Moroka, 1300 m., New Guinea. July to November, Loria (our determination)

PLATE V

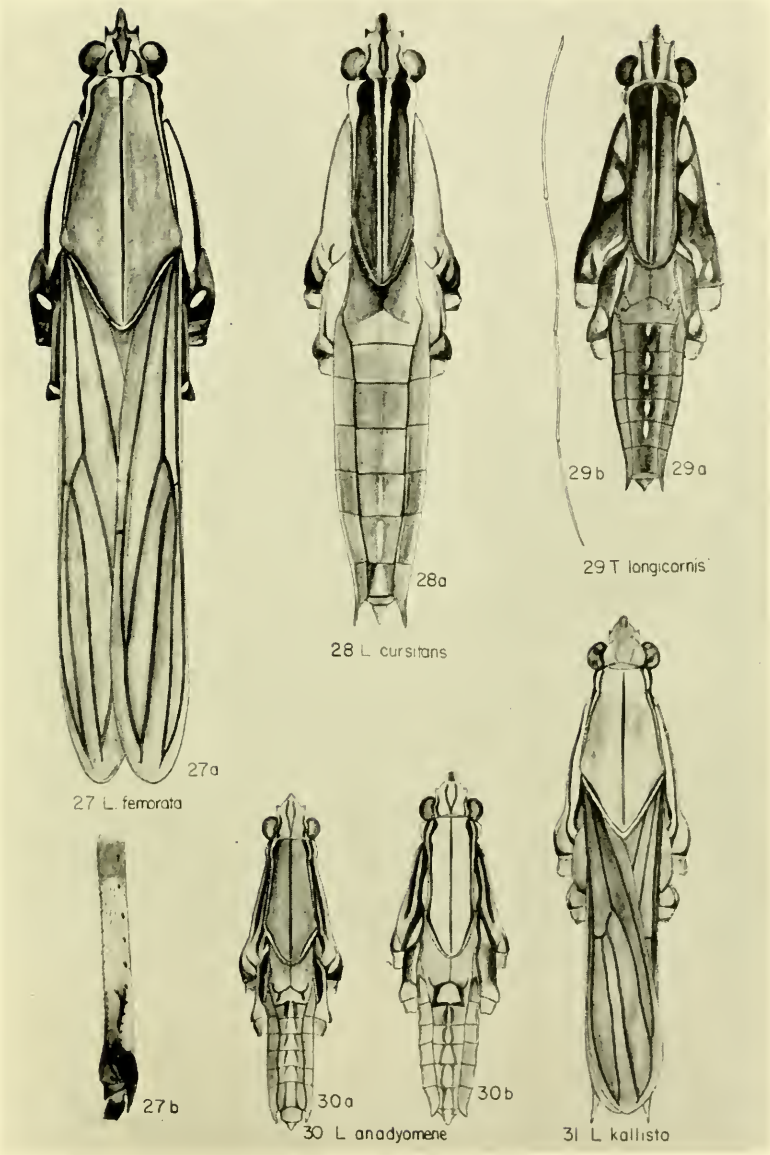

27a
27 L. femorata
27b
28a
28 L. cursitans
29b
29a
29 T. longicornis
30a
30b
30 L. anadyomene
31 L. kallisto

PLATE VI

FIG. 32. *Tenagogonus grandiusculus* Poisson
Wingless male. Sangmelina, Cameroons, W. Africa. Apr. 16, 1932, A. I. Good. This male was determined by us as *T. longicornis* Poisson. However, the female accompanying this specimen was determined by Poisson as *T. grandiusculus* Poisson.

PLATE VI

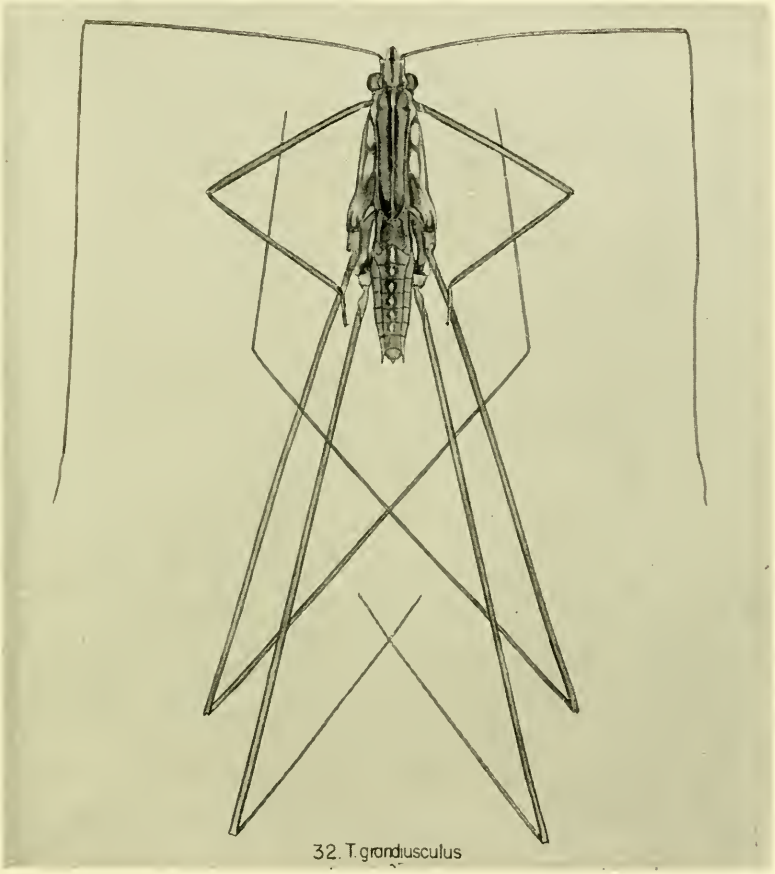


PLATE VII

FIG. 1. *Tenagogonus albovittatus* Stål

a. Dorsal view of the tip of female abdomen. Sangmelina, Cameroons, W. Africa. Oct. 14, 1934. A. I. Good (Compared with type by Lundblad.)

b. Ventral view of the tip of male abdomen. The same data as above.

c. Lateral view of the tip of male abdomen. The same data as above.

FIG. 2. *Tenagogonus zambezinus* Poisson?

a. Ventral view of the tip of female abdomen. Nagana Res. Lab. Zululand. Apr. 22, 1922, H. H. Curson

b. Lateral view of the tip of male abdomen. S. Rhodesia, S. Africa. 1928-1935, G. E. Hutchinson

c. Ventral view of the tip of male abdomen. The same data as b.

FIG. 3. *Tenagogonus madagascariensis* Hoberlandt

a. Ventral view of the tip of female abdomen. Tananarive, Madagascar 1937 (paratype)

b. Ventral view of the tip of male abdomen. The same data as above. (paratype)

c. Lateral view of the tip of male abdomen. The same data as above.

FIG. 4. *Tenagogonus kampaspe* (Kirkaldy)

a. Ventral view of the tip of female abdomen. Rigo, New Guinea mer., July, 1889. L. Loria (type series)

b. Ventral view of the tip of male abdomen. The same data as above.

c. Lateral view of the tip of male abdomen. The same data as above.

FIG. 5. *Tenagogonus divergens* Hungerford

a. Lateral view of the tip of abdomen. Brook near Bawomataluwo, Sumatra. Dec. 9, 1931, v. d. Meer Mohr (type)

PLATE VII

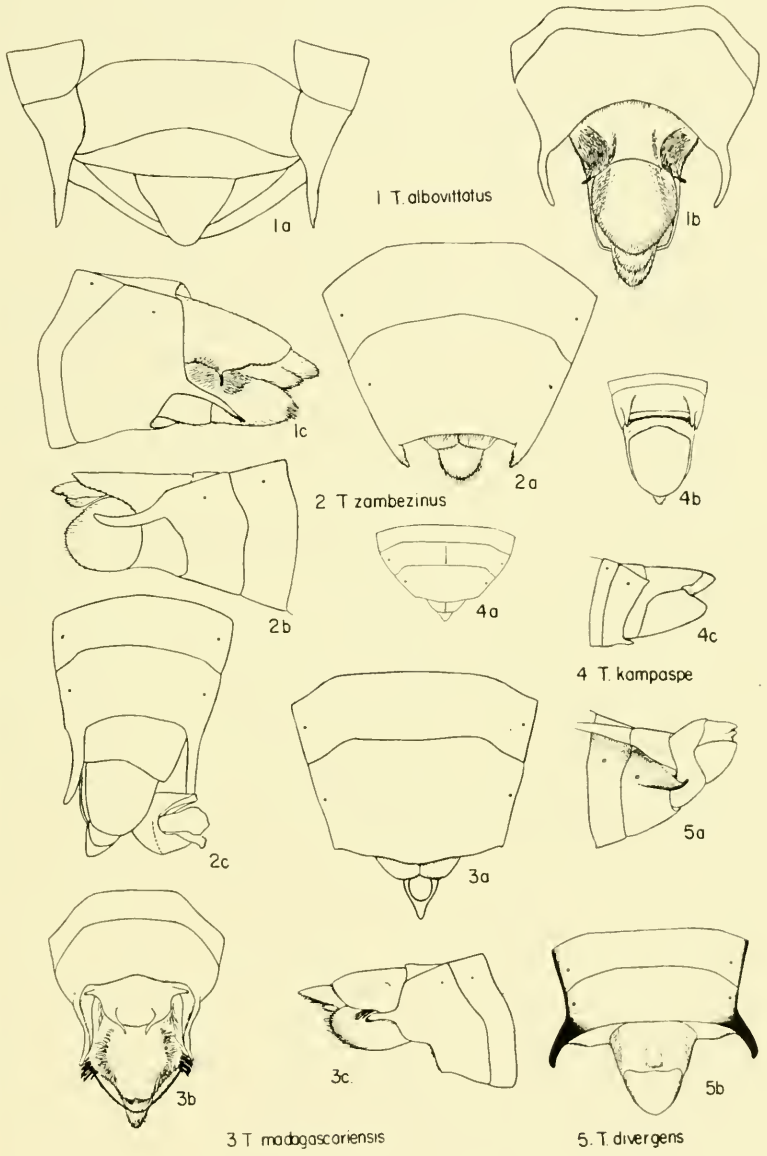

1a
1 T. albovittatus
1b
1c
2a
2 T. zambezinus
4b
2b
4a
4c
4 T. kampaspe
2c
3a
5a
3b
3c
5b
3 T. madagascariensis
5. T. divergens

PLATE VIII

FIG. 6. *Tenagogonus brevis* (Lundblad)

a. Ventral view of the tip of female abdomen. Java, Thienemann (allotype)

FIG. 7. *Tenagogonus fijiensis* Hungerford and Matsuda

a. Lateral view of the tip of female abdomen. Fiji Island. July, 1934, R. W. Paine (type series)
b. Dorsal view of the tip of female abdomen. The same data as above.
c. Ventral view of the tip of male abdomen. The same data as above.
d. Lateral view of the tip of male abdomen.

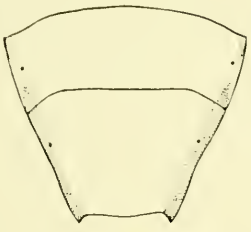
FIG. 8. *Tenagogonus pravipes bergrothi* Hungerford and Matsuda

a. Ventral view of the tip of male abdomen. Observatory Garden, Manila, Philippine Islands. (type series)
b. Dorsal view of the tip of male abdomen. The same data as above.
c. Dorsal view of the tip of female abdomen. The same data as above.
d. Ventral view of the tip of female abdomen. The same data as above.

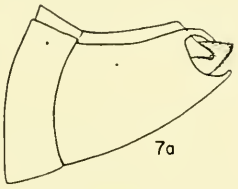
FIG. 9. *Tenagogonus robustus* Hungerford and Matsuda

a. Ventral view of the tip of male abdomen. Pogobina, W. Sumba. Sept. 17, 1949, D. Bühler, Dr. Sutter (type series)
b. Lateral view of the tip of male abdomen. Prai Jawang, East Sumba. June 14, 1949, Dr. Bühler, Dr. Sutter.
c. Ventral view of the tip of female abdomen. The same data as above.

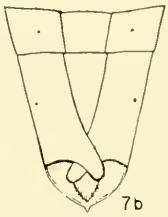
PLATE VIII

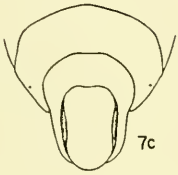


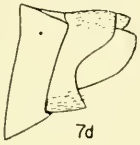
6. T. brevis

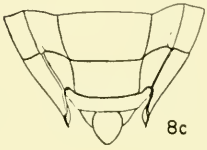


7. T. fijiensis

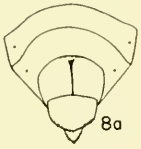


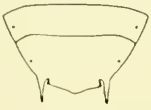




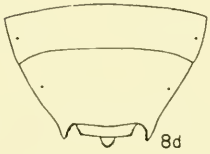


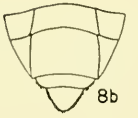
8 T. pravipes bergrothi

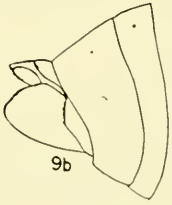


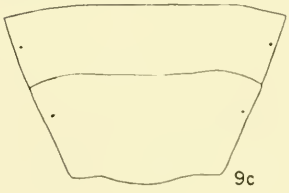


10 T. r. claggi









9. T. robustus

PLATE IX

FIG. 11. *Tenagogonus kuiterti* Hungerford and Matsuda

a. Dorsal view of the tip of wingless male abdomen. Burma. 1944, L. Kuitert (type series)
b. Ventral view of the tip of wingless male abdomen. The same data as above.
c. Lateral view of the tip of wingless male abdomen. The same data as above.
d. Lateral view of the tip of winged male abdomen. Mohnylin, Burma, Oct. 27, 1944, L. Kuitert
e. Ventral view of the tip of winged male abdomen. The same data as above.
f. Dorsal view of the tip of wingless female abdomen. The same data as above.
g. Ventral view of the tip of wingless female abdomen. The same data as above.
h. Ventral view of the tip of winged female abdomen. The same data as above.

FIG. 12. *Limnometra lipovskyi* Hungerford and Matsuda

a. Ventral view of the tip of female abdomen. Guadalcanal Island. Jan. 1945, L. J. Lipovsky (type series)
b. Lateral view of the tip of male abdomen. The same data as above.
c. Ventral view of the tip of male abdomen. The same data as above.

PLATE IX

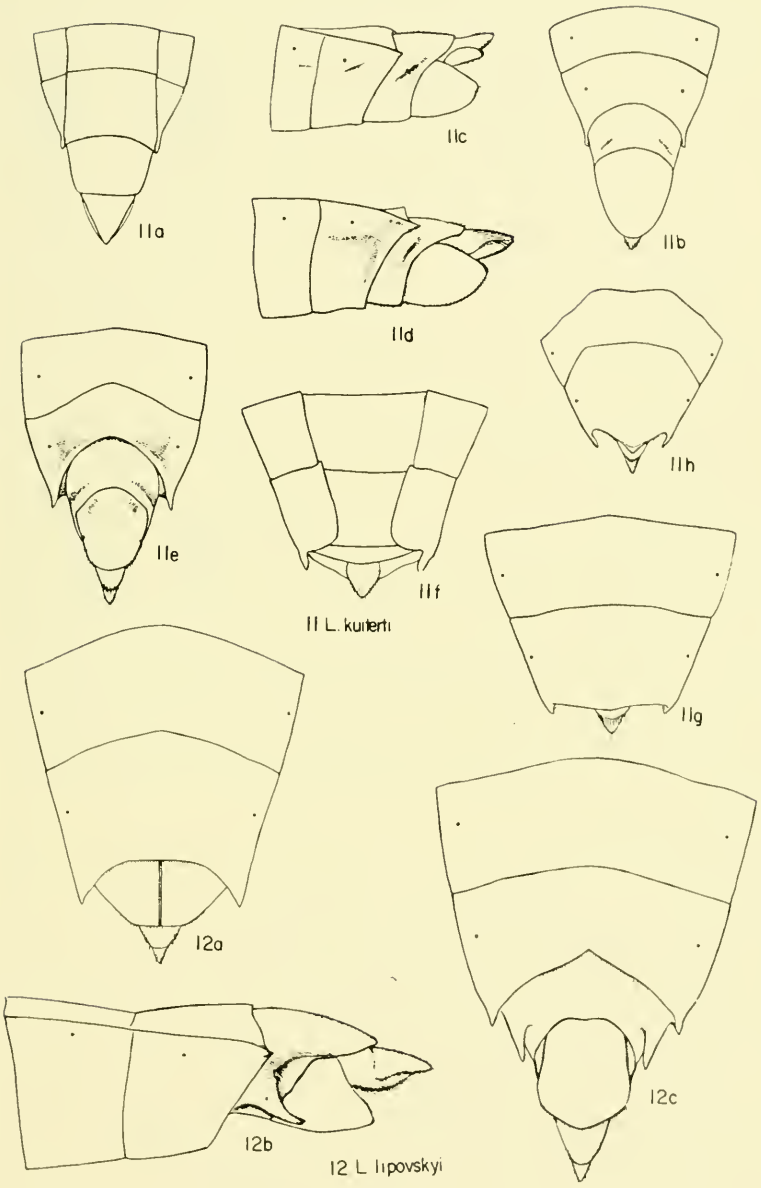

11a
11c
11b
11d
11h
11e
11f
11 L. kuiferti
11g
12a
12c
12b
12 L. lipovskyi

PLATE X

FIG. 13. *Limnometra octopunctata* Hungerford

a. Ventral view of the tip of male abdomen. Tandjong Morawa, Serdang, N. O. Sumatra (holotype)

b. Dorsal view of the tip of male abdomen. The same data as above.

c. Dorsal view of the tip of female abdomen. The same data as above. (allotype)

d. Ventral view of the tip of female abdomen. The same data as above. (allotype)

FIG. 14. *Limnometra minuta* Mayr

a. Ventral view of the tip of male abdomen. Novara Expedition, Sambelong (type)

FIG. 15. *Limnometra fluviorum* (Fabricius)

a. Ventral view of the tip of female abdomen. Tanjore Dist. India. P. Susai Nathan

b. Lateral view of the tip of male abdomen. The same data as above.

c. Ventral view of the tip of male abdomen. The same data as above.

PLATE X

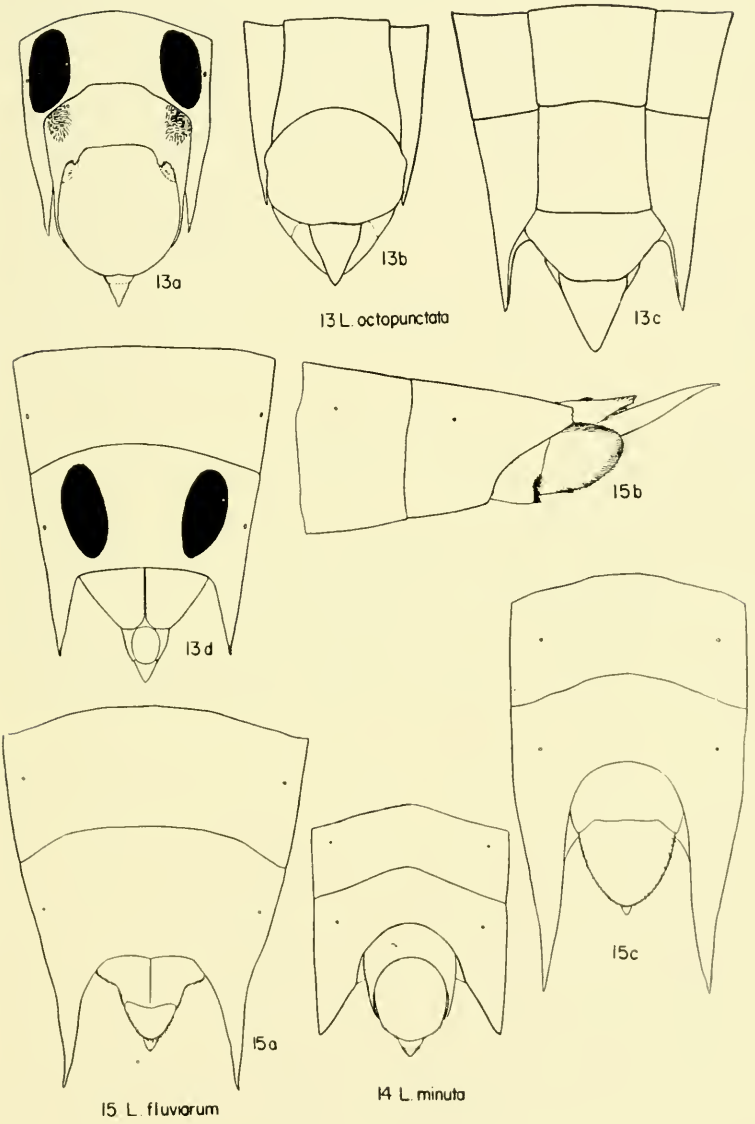

13a
13b
13 L. octopunctata
13c
13d
15b
15c
15a
15 L. fluviorum
14 L. minuta

PLATE XI

FIG. 16. *Limnometra anadyomene* (Kirkaldy)

a. Lateral view of the tip of male abdomen. Punduloya, Ceylon. E. E. Green (type series)
b. Ventral view of the tip of female abdomen. The same data as above.
c. Dorsal view of the tip of female abdomen. The same data as above.

FIG. 17. *Limnometra insularis* Hungerford and Matsuda

a. Ventral view of the tip of male abdomen. Tandjong Morawa, Serdang, N. E. Sumatra. Dr. B. Hagen (holotype)
b. Lateral view of the tip of male abdomen. The same data as above.
c. Ventral view of the tip of female abdomen. The same data as above.

PLATE XI

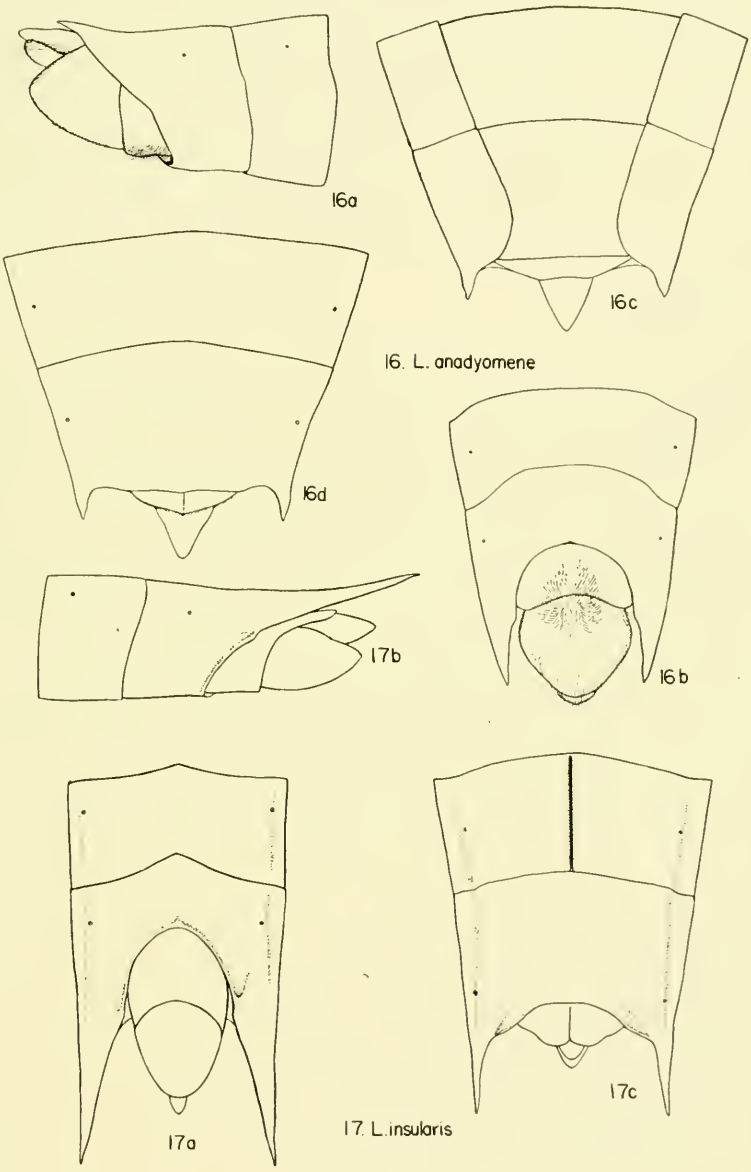


PLATE XII

FIG. 18. *Limnometra palauana* Esaki

a. Lateral view of the tip of abdomen. Toloas, Truk, Caroline Islands. Jan. 21, 1938, T. Esaki (type series?)
b. Ventral view of the tip of abdomen. The same data as above.
c. Lateral view of the tip of abdomen. The same data as above.
d. Ventral view of the tip of abdomen. The same data as above.

FIG. 19. *Limnometra borneensis* Hungerford and Matsuda

a. Ventral view of the tip of male abdomen. Mt. Pol. Sarawak, Borneo. (type series)
b. Lateral view of the tip of male abdomen. The same data as above.
c. Ventral view of the tip of female abdomen. The same data as above.

FIG. 20. *Limnometra rossi* Hungerford and Matsuda

a. Lateral view of the tip of male abdomen. San José, Mindoro, Philippine Islands. Apr. 1945, E. S. Ross (type series)
b. Ventral view of the tip of male abdomen. The same data as above.
c. Ventral view of the tip of female abdomen. The same data as above.

PLATE XII

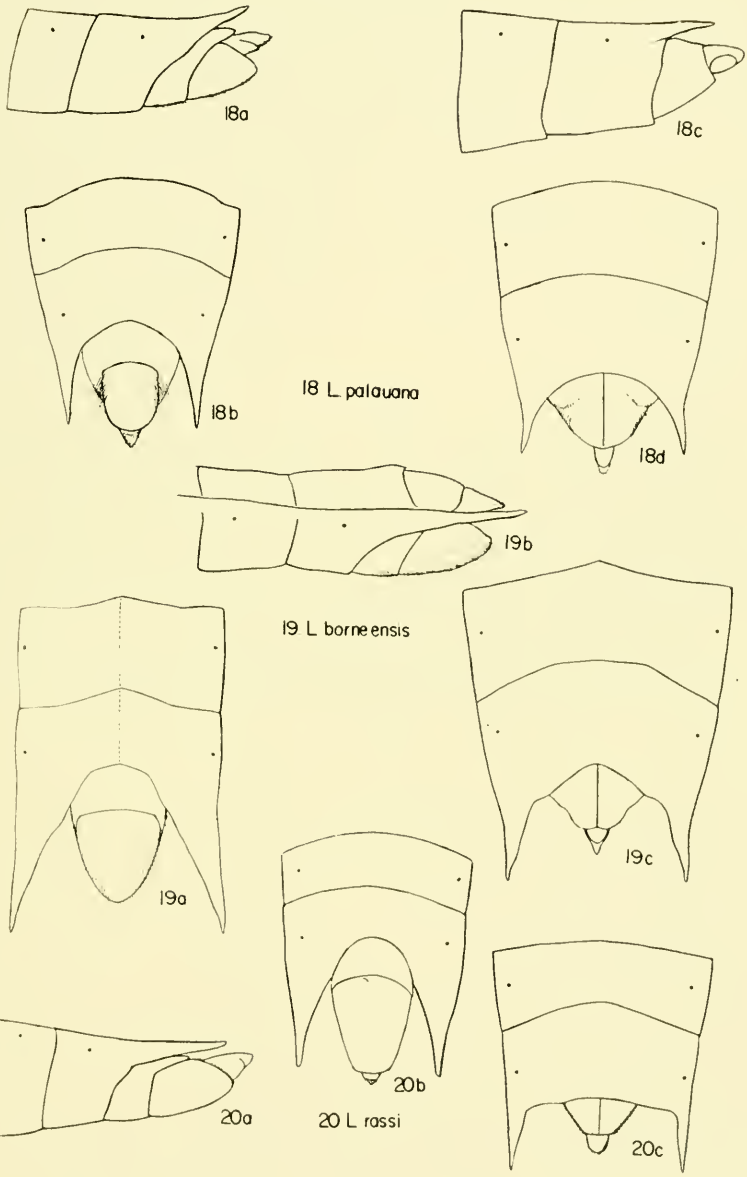

18a
18c
18b
18 L. palauana
18d
19b
19 L. borneensis
19a
19c
20b
20a
20 L. rossi
20c

PLATE XIII

FIG. 21. *Limnometra femorata* Mayr

a. Ventral view of the tip of male abdomen. E. slope, Mt. McKinley, Davao province, Philippine Islands, 1946-47, F. G. Werner

b. Lateral view of the tip of male abdomen. The same data as above.

c. Ventral view of the tip of female abdomen. The same data as above.

FIG. 22. *Limnometra ciliata* (Mayr)

a. Ventral view of the tip of female abdomen. Samanga, S. Celebes. Nov. 1893, H. Fruhstorfer

b. Dorsal view of the tip of male abdomen. Sumbawa

c. Lateral view of the tip of male abdomen. The same data as b.

d. Ventral view of the tip of male abdomen. The same data as b.

PLATE XIII

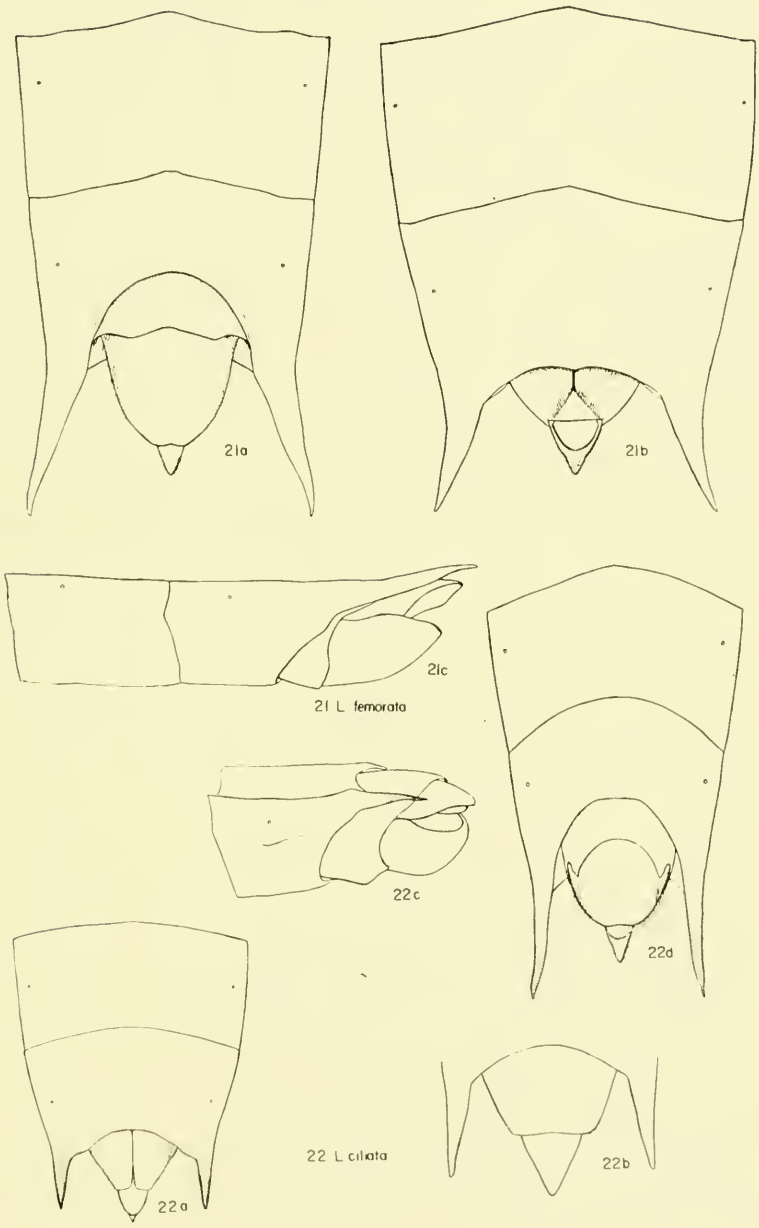


PLATE XIV

FIG. 23. *Limnometra cursitans* (Fabr.)

a. Dorsal view of the tip of female abdomen. Merauke, Dutch New Guinea. Mar. 27, 1939, R. G. Wind
b. Ventral view of the tip of female abdomen. The same data as above
c. Ventral view of the tip of winged male abdomen. The same data as above
d. Lateral view of the tip of male abdomen. The same data as above
e. Ventral view of the tip of wingless male abdomen. The same data as above

FIG. 24. *Limnometra nigripennis* Mayr

a. Ventral view of the tip of female abdomen. Samar Island. Baker
b. Dorsal view of the tip of female abdomen. The same data as above
c. Ventral view of the tip of male abdomen. Philippine (type)

PLATE XIV

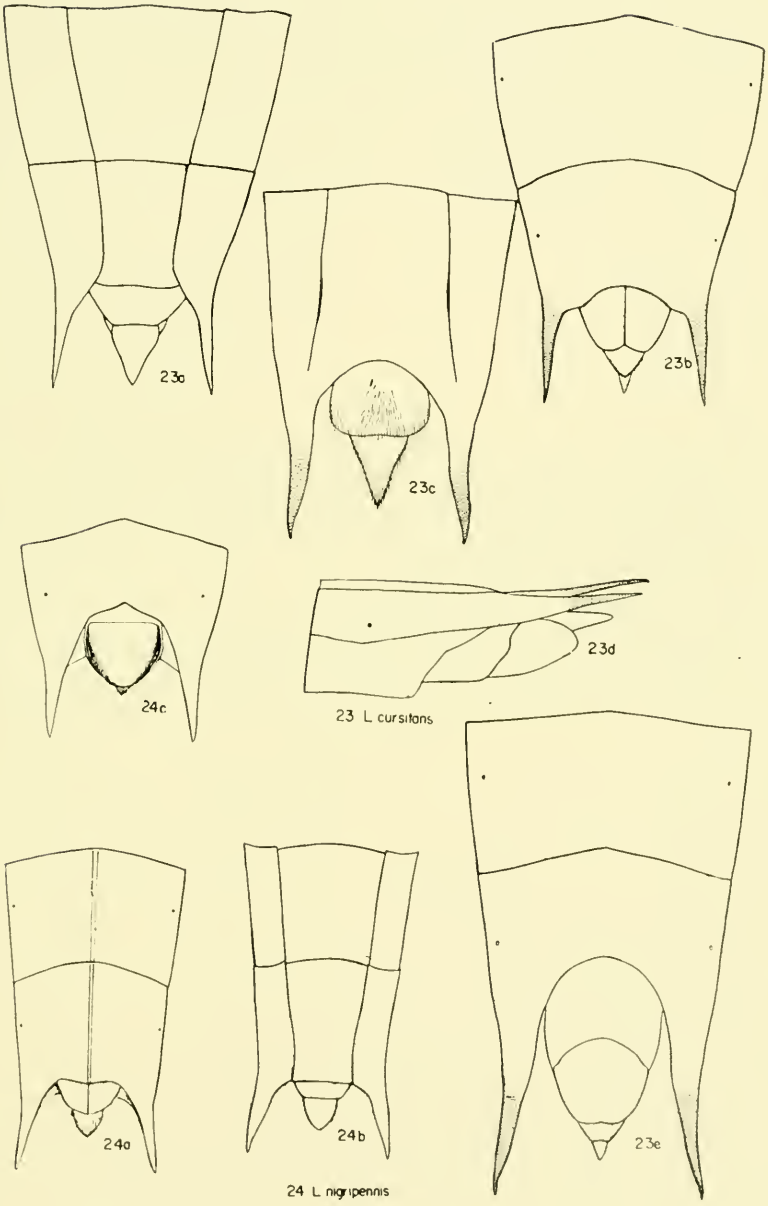

23a
23c
23b
24c
23d
23 L. cursitans
24a
24b
23e
24 L. nigripennis

PLATE XV

FIG. 25. *Limnometra pulchra* (Mayr)

a. Ventral view of the tip of female abdomen. Amboina (type series)
b. Lateral view of the tip of male abdomen. The same data as above
c. Ventral view of the tip of male abdomen. The same data as above
d. Apical part of male front femur
e. Apical part of male middle femur

FIG. 26. *Limnometra annulicornis* Breddin

a. Ventral view of the tip of male abdomen. Celebes (type series)
b. Lateral view of the tip of male abdomen. The same data as above
c. Ventral view of the tip of female abdomen. The same data as above

PLATE XV

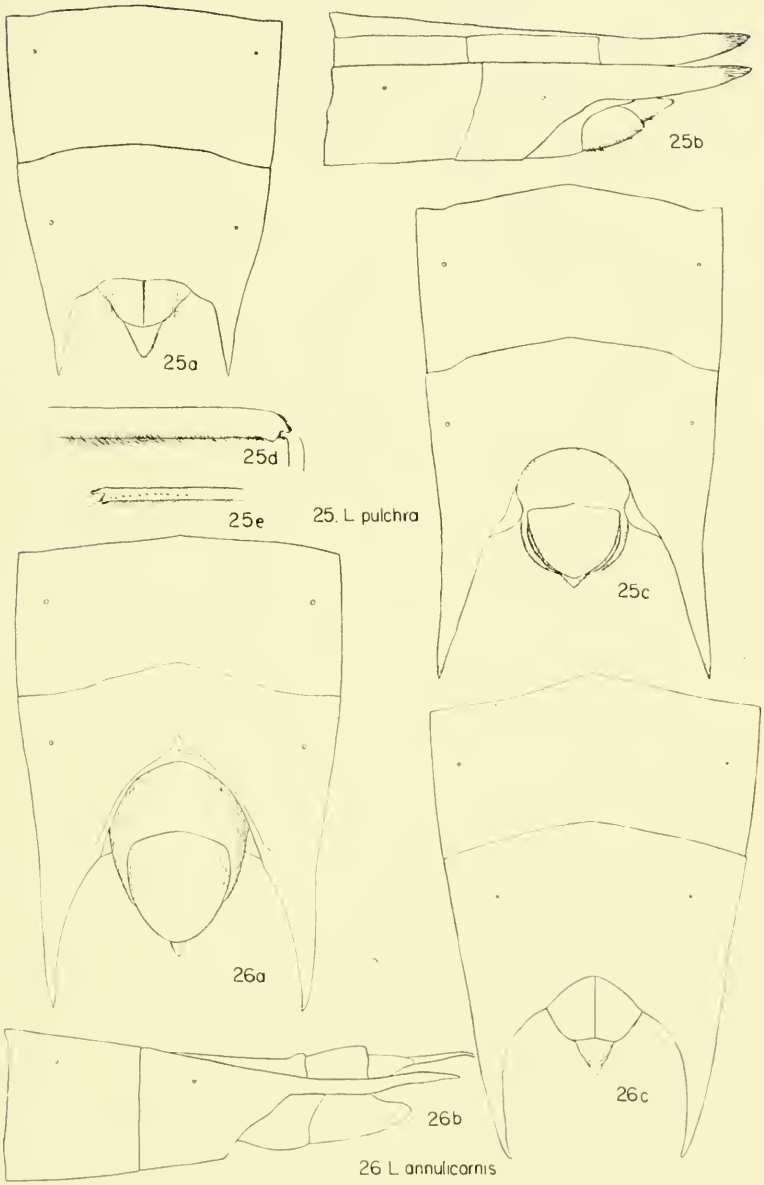


PLATE XVI

FIG. 27. *Limnometra kallisto* (Kirkaldy)

a. Ventral view of the tip of female abdomen. New Guinea. Beccari, 1875 (Det. by Kirkaldy.)

b. Lateral view of the tip of female abdomen. The same data as above

FIG. 28. *Limnometra palauana* Esaki?

a. Ventral view of the tip of female abdomen. Los Negros, Admiralty Island. Aug. 11, 1945. P. J. Ribert

b. Ventral view of the tip of male abdomen. The same data as above

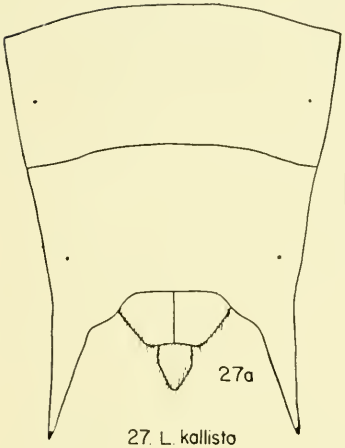
c. Lateral view of the tip of male abdomen. The same data as above

FIG. 29. Metasternum of *Gigantometra gigas* (China). Ta Han, Hainan, China. June 24, 1935

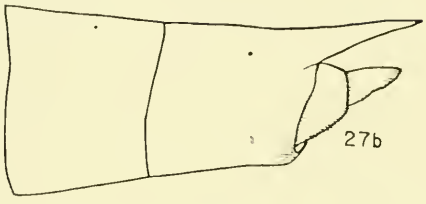
FIG. 30. Metasternum of *Tenagogonus robustus* Hungerford and Matsuda. Prai Jawang, East Sumba. June 14, 1949. Dr. Bühler, Dr. Sutter

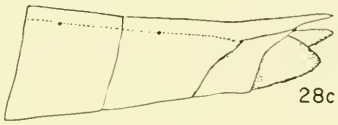
FIG. 31. Metasternum of *Tenagogonus grandiusculus* Poisson. Sangmelina, Cameroons, W. Africa. Apr. 16, 1932, A. I. Good

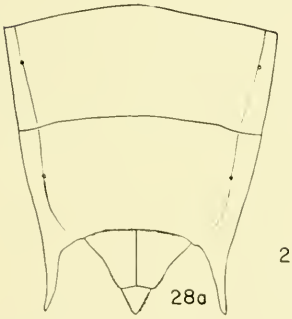
PLATE XVI



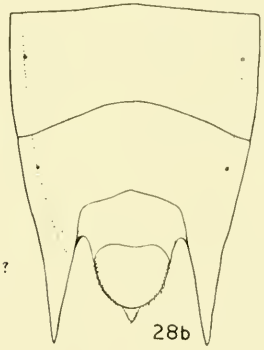
27. L. kallisto

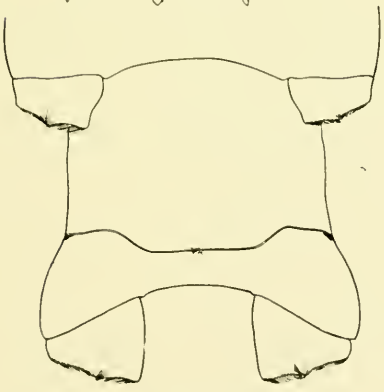






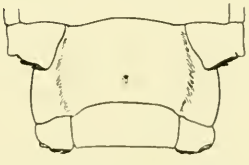
28 L. palauana?





29. G. gigas

30. T. robustus



31 T. grandiusculus

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

VOL. XXXIX] NOVEMBER 18, 1958 [NO. 10

An Anatomical Study of a Neotropical Tree Frog, *Centrolene prosoblepon* (Salientia: Centrolenidae)

BY

THEODORE H. EATON, JR.

ABSTRACT: The osteology and major features of the myology of *Centrolene prosoblepon* are described, and the position of the Centrolenidae is considered. The family appears to be an offshoot from a Neotropical group of *Hyla* in which the following characters are present: dorsal color green; forearm relatively large, especially in male; eyes large and directed about 45° forward; bones green; femur with a low posterior crest. To these features the following, distinctive of Centrolenidae, are added as specializations: fusion of tibiale and fibulare into one bone; a basal pad on the palm; T-shaped terminal phalanges (the latter independently of their occurrence elsewhere among frogs.)

INTRODUCTION

The family Centrolenidae was proposed by Taylor (1951) for a group of small Neotropical tree frogs in which the tibiale and fibulare (astragalus and calcaneum) are fused into a single bone. Usually the terminal phalanges are T-shaped, and the palm has a basal pad. In these features the family differs from Hylidae, but it resembles the latter in other respects: intercalary cartilage between terminal and penultimate phalanges; procoelous vertebral column with double condyle on sacrum, dilated sacral diapophyses; arciferal pectoral girdle. Many of the species of Centrolenidae so far known are Costa Rican (Taylor, 1952), but the family extends from Mexico to southern Brazil (Taylor and Cochran, 1953).

The general appearance of frogs in this family is shown by Fig. 1, the photograph of a male and female of *Centrolene prosoblepon*. In life they are green to cream-color dorsally, yellowish or whitish ventrally, but in alcohol the dorsal pigment becomes lavender or pink; the same is true of certain Hylidae (*Agalychnis, Phyllomedusa*, and a few species of *Hyla*, as *H. alleei*). In both sexes, but most

FIG. 1. Male (below) and female (above). This and all following figures are of *Centrolene prosoblepon* (Boettger). Photograph by courtesy of Professor E. H. Taylor.

obviously in the male, the forearm is massive as compared with the slim upper arm, and in preserved specimens it is difficult to force extension of the elbow without breaking the arm; this peculiarity is seen likewise in the above-mentioned Hylids. A striking feature of the Centrolenids is the nearly transparent skin, through which one may see muscles, nerves, parts of the skull, and

even the brain. The bones are often green. (See Fig. 2 for details of dorsal and ventral surfaces.)

Three genera are recognized. *Centrolene*, normally with vomerine teeth, is peculiar in having a hooklike spine on the lateral face of the humerus in the males (as does the Australian *Hyla humeralis*). *C. prosoblepon* (Boettger) is the only species in Costa Rica. The males of *Teratohyla* (one species, *spinosa*) have a sharp spine on the prepollex; this may or may not project through the skin. Vomerine teeth are present but very small in *Teratohyla*. Of the Costa Rican species of *Cochranella, granulosa, albomaculata* and *pulverata* have vomerine teeth and about as much pigmentation as *Centrolene*. The remaining species, lacking vomerine teeth, tend also to reduce their pigmentation. The tympanum is still readily visible in *C. valerioi, talamancae* and *colymbiphyllum*, but is reduced and largely concealed under the skin in *chrysops* and *fleischmanni*. Evidently, then, the major group is the genus *Cochranella*, from which *Teratohyla* differs in possessing the prepollical spine, and *Centrolene* in having a humeral spine, both of these being specializations of the male.

FIG. 2. Details of ventral (left) and dorsal (right) surfaces of male, K. U. catalog No. 11202. × 2.

ACKNOWLEDGMENTS

To Professor Edward H. Taylor I am indebted for the opportunity to study these remarkable little frogs, including examination of all the species named above as well as certain others not yet published; also for information regarding their habits and appearance in life, and for the use of the photograph, Fig. 1. With his permission and that of John M. Legler, curator of the herpetological collections at Kansas University, I have dissected a male and female of *Centrolene prosoblepon* and examined skeletons of this and numerous species of Central American Hylidae. (Data on the dissected specimens are as follows: Male, catalog No. 37016, coll. by E. H. Taylor, Cinchona, Heredia Prov., Costa Rica, July 12, 1954. Female, catalog No. 32385, coll. by E. H. Taylor, near Pacayas, Costa Rica, July 2, 1952.) I wish to thank Professor E. Raymond Hall for use of the facilities of the Natural History Museum while I was Visiting Professor at Kansas University during the summer of 1957.

OSTEOLOGY

Skull (Figs. 3, 4). In correlation with the diminutive size of *Centrolene prosoblepon* (male snout-vent length 24.7 mm.), its skull shows reduction in the number and degree of ossification of bones as compared, for example, with *Rana*. This is especially evident in the cranium, where the otic capsules, frontoparietals, occipitals and parasphenoid all are fused, with no distinguishable sutures, and parts of the otic and ethmoid regions are cartilaginous. There is a large median dorsal fenestra, occupied by a slightly flexible sheet of connective tissue; through this the cerebral hemispheres are visible. Positions of the three semicircular canals show clearly by reduction of the bone enclosing them, so that they are outlined by protruding ridges. In the dry skull the limits of the parasphenoid, frontoparietals, palatines, vomers and ethmoid cannot be distinguished, but in dissection, using Clorox to clear connective tissue from the surface, it was possible to see some faint sutures or margins of ossification, as shown in the figures.

From the lateral edge of the otic capsule the slender squamosal extends forward to the posterior margin of the orbit, and also sends a narrow process down on the side of the quadrate. Between the squamosal and the ossified portion of the otic capsule is a zone of cartilage, not evident in the dry skull. The stapes, ossified superficially, lies just ventral to the rim of this cartilage on its posterior side, and is quite firmly fixed in the fenestra ovalis. The distal end

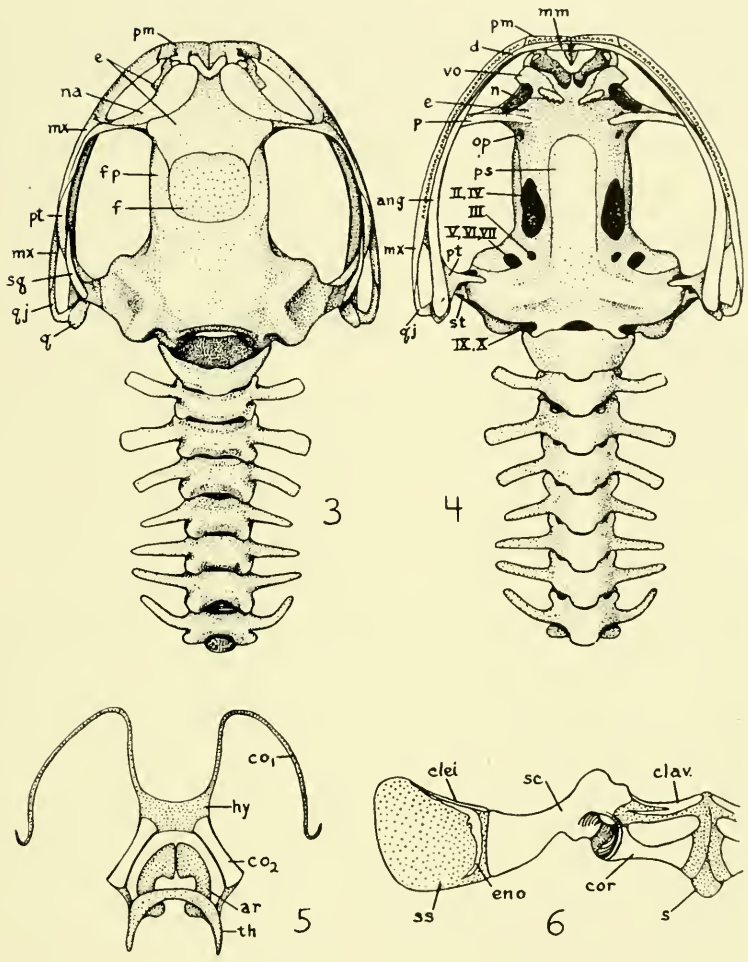


FIG. 3. Skull and first eight vertebrae of male, skeleton No. 41054, dorsal aspect, × 10.

FIG. 4. Same, ventral aspect.

FIG. 5. Hyoid apparatus of male, No. 11202, ventral aspect, × 10.

FIG. 6. Right half of pectoral girdle, shown as flattened, male, No. 11202, ventral aspect, × 10.

of the stapes reaches the dorsal margin of the tympanum rather than the center, and it seems doubtful that this bone can have much value in sound transmission. It may be on the way toward a degeneration which is reflected in the concealment of the tympanum under the skin in some species of *Cochranella*. The tympanic ring is weak and comes off with the skin in dissection. There is an ossi-

fied operculum, and the white otolith is visible through the posterior wall of the otic capsule.

Bones of the upper jaw are supported by the quadrate, only partly ossified, and by the pterygoid, extending forward to meet the maxillary along the lower margin of the orbit. Between the quadrate and the posterior end of the maxillary is a slender quadratojugal. In front of the orbit the maxillary sends a preorbital process dorsomedially to meet the nasal and ethmoid. The premaxillaries articulate by narrow ascending processes with the nasals and also with the delicate cartilage rims of the ethmoid. Teeth are present as shown in the maxillary and premaxillary; there is some evidence of replacement in the anterior part of the series, where a partial second row can be seen in the bones. The vomerine teeth are borne on short ridges medial to the internal nares, and number three or four in each fascicle.

The foramina for cranial nerves are similar to those in *Rana*, except that a large fenestra incorporates both the optic and trochlear foramina; it is covered largely by connective tissue.

The mandible is composed of Meckel's cartilage, enlarged proximally to make the articulation with the quadrate, and ossified only near the symphysis, as a small mentomeckelian bone. A thin dentary covers the cartilage anteriorly, and the angular does so over most of the posterior and medial surfaces, but these bones do not quite meet each other.

The hyoid apparatus (Fig. 5) resembles, but is simpler than, that figured by Romer (1955, Fig. 143C) for *Leptodactylus*. The anterior horn, exceedingly delicate and flexible, curves forward as far as the posterior edge of the tongue; it then recurves behind the end of the mandible, medial to the depressor mandibulae, and is attached to the lower wall of the otic capsule close to the stapes. The body of the hyoid is a thin cartilage plate receiving the posterior ends of muscle strands from the tongue. On its posterior corners are the two bony horns (first branchials). The arytenoid cartilages enclose the larynx on each side, meeting ventrally. The thyroid cartilage is a thin, delicate ventral arch ending laterally in two fairly firm horns attached to the pericardium. There is no cricoid cartilage. (In *Leptodactylus*, as cited above, a cricoid is present and the body of the hyoid bears two pairs of lateral processes.)

Vertebral Column (Figs. 3, 4, 7, 8). Little needs to be added to the details figured. There are no neural spines, and the atlas

lacks transverse processes. The centra (Fig. 4) are procoelous, the sacrum has two condyles for the coccyx (Fig. 8), and the sacral diapophyses are slightly dilated. In these points and in the particular form and position of the transverse processes the Centrolenid frogs are precisely like the smaller species of *Hyla*. The figures of the pelvis (Figs. 7, 8) are self-explanatory.

Pectoral Girdle (Fig. 6). In this figure the cartilage is stippled. The sternum is a thin, fragile sheet. The cartilaginous medial ends of the coracoids overlap in the usual arciferal manner except at their anterior ends, where they fuse between the clavicles. A zone of cartilage intervenes between the ossified coracoid and scapula at the glenoid fossa, and there is a small glenoid foramen. The suprascapula bears a splinterlike cleithrum on its anterior edge, and has also a narrow irregular zone of endochondral ossification. Dorsally the suprascapula overlaps, and is fastened by connective tissue to, the tip of the first transverse process (second vertebra). This gives the pectoral girdle rigidity in the body of the frog.

Arm and Hand (Figs. 9, 10, 11). There is little difference between the male (shown in the figures) and female, except in the humerus. This bears a prominent thin spine on its lateral face in the male, so placed that it opposes the medial face of the thumb when the forearm is flexed and the hand adducted. Presumably the spine is involved mechanically in amplexus, but no observations of this have been made. The spine is occasionally present in females, normally absent. In addition, the humerus in the male has two crests on its posterior face distally (Fig. 9), the more ventral of which is for the origin of the flexor carpi radialis muscle, and the dorsal one, slightly smaller, for that of the extensor carpi radialis. Between the two crests lies the distal portion of the anconeus. These crests are faintly or not at all indicated in the female, and the associated muscles are much smaller. It should be noted that *Centrolene* is not unlike many other frogs in regard to the crests; Ritland (1955) describes a similar condition in *Ascaphus*.

On the ventral surface of the humerus there is also a conspicuous groove for the tendon of the coracoradialis muscle (Fig. 10). This muscle, with its tendon, is one of the most constant features of both frogs and salamanders. The groove is deepest and broadest near the head of the humerus; lateral to it, at the base of the spine, is a rounded ridge for the insertion of the more superficial muscles of the pectoral group.

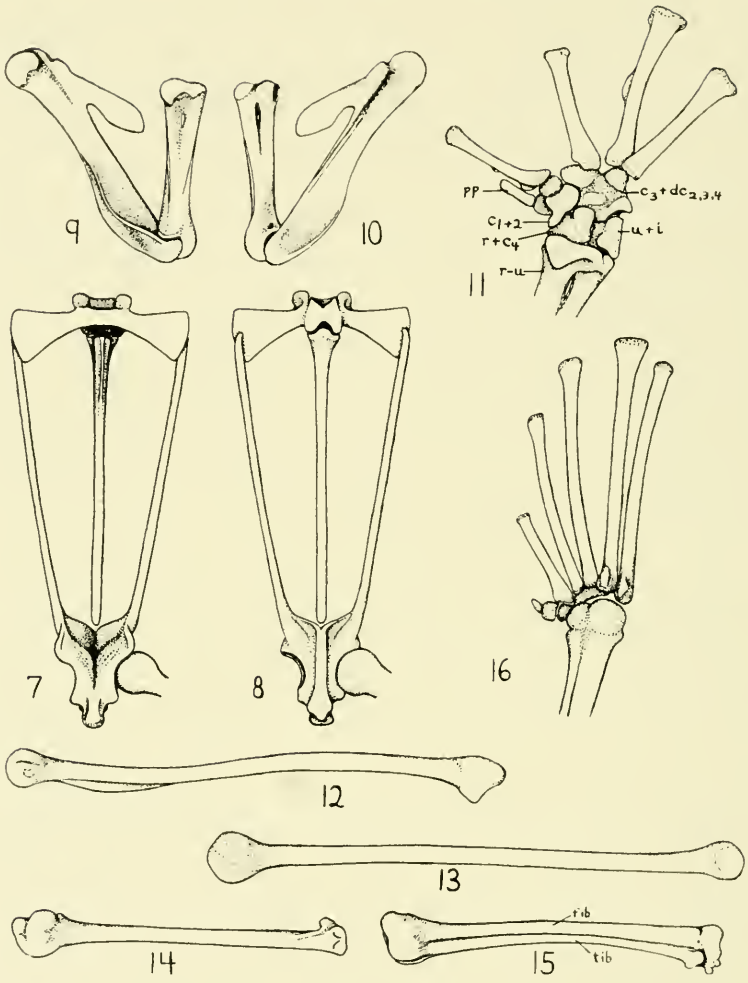


FIG. 7. Sacrum, coccyx and pelvis, male, skeleton No. 41054, dorsal aspect, × 5.

FIG. 8. Same, ventral aspect.

FIG. 9. Right humerus and radioulna, male, skeleton No. 41054, dorsal aspect, × 5.

FIG. 10. Same, ventral aspect.

FIG. 11. Right carpus, male, No. 11202, dorsal aspect, × 8.

FIG. 12. Right femur, male skeleton No. 41054, dorsal aspect, proximal end to left, posterior border down, × 5. (Figs. 13-15 are from same skeleton, same magnification.)

FIG. 13. Right tibiofibula, dorsal aspect, proximal end to left.

FIG. 14. Right tibiale-fibulare (astragalo-calcaneum), postaxial aspect, proximal end to left.

FIG. 15. Same, plantar aspect.

FIG. 16. Right tarsus, male, No. 11202, dorsal aspect, × 8.

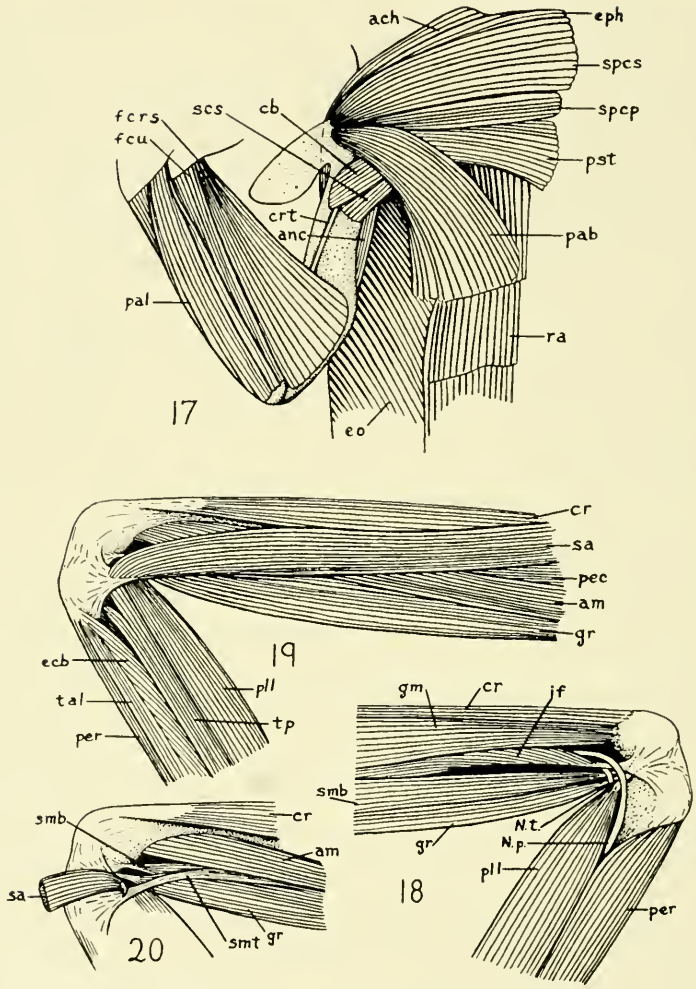
A special feature of the radioulna is the small open cleft which persists between the shafts of the radius and ulna where they have not fused completely, near the distal end.

The skeleton of the carpus (Fig. 11) is essentially as in *Rana*. Following Ritland (1955) I am calling the "thumb" the first digit, and the small bone lying against the base of it the prepollex. The only entirely cartilaginous pieces are two distal carpals, one at the base of the prepollex, the other at the base of the first metacarpal. There are four other highly irregular and mostly ossified elements. The two proximal ones probably represent (a) ulnare + intermedium fused, on the ulnar side, and (b) radiale + centrale 4, on the radial side. Distal to the latter is a piece (c) which is probably centrale 1 + 2. The largest and most complex (d) is that which provides a base for metacarpals 2, 3 and 4. It probably comprises centrale 3 + distal carpals 2, 3 + 4. These inferences are based on the positions and shapes of the pieces, but confirmation from developmental stages would be desirable.

The phalanges, not figured, number 2, 2, 3, 3 in the fingers. They, like the metacarpals, are ossified in a surface layer but apparently not internally, and have cartilaginous tips at each joint. The terminal ones have narrow distal extensions giving them a T-shape, unlike those of Hylidae. Each digital pad is supported by, and encloses, such a T-shaped phalanx, and a small round intercalary cartilage fits between that and the next proximal to it, as in Hylids.

Leg and Foot (Figs. 12-16). In contrast to the fore limb and hand the hind leg appears long, slender and delicate, and this is shown also in the proportions of the bones. The most distinctive feature of the femur (Fig. 12) is a low, thin crest on the posterior side near the base. This is not the usual crista femoris, which is lacking. The posterior crest has the insertion of the obturator externus muscle on its ventral surface, and of the quadratus femoris (more posterior) and gemellus (more anterior) on the dorsal. This crest is also present in the following small species of *Hyla*, of which I have seen skeletons: *alleei, elaeochroa, loquax, phlebodes, pseudopuma,* and *rufioculis,* all from Costa Rica, but it is lacking in a number of larger species.

The tibiofibula (Fig. 13) is nearly straight and slightly longer than the femur. The union of tibiale and fibulare into one bone (Figs. 14-16), the principal character on which the family Centrolenidae is based, might be described as a partial fusion in *Centrolene,* for the shafts are almost separate and retain their individual



Muscles of male, No. 11202, × 8.

FIG. 17. Pectoral region and arm, ventral aspect.
FIG. 18. Right knee, dorsal aspect.
FIG. 19. Right knee, ventral aspect, superficial.
FIG. 20. Same, the sartorius reflected to show tendons.

shape, while the heads are more completely fused. There remains in the tarsus proper a minute prehallux, a cartilaginous tarsal accompanying it, another tarsal also of cartilage which is associated with the first metatarsal, and a narrow crescent-shaped cartilage probably representing a fusion of tarsals 2 + 3 or 2 + 3 + 4. A

ligamentum tarsi supplens is present in the position indicated by a gap in Fig. 16, but it contains no cartilage. The tips of all the metatarsals are of cartilage. The phalangeal formula in the toes is 2, 2, 3, 4, 3. Otherwise all remarks about the phalanges and digits in the hand apply also to those in the foot.

MYOLOGY

Certain portions of the muscular systems were dissected and illustrated, but time did not permit a full description of the muscles. In Fig. 17 a ventral view of the pectoral and fore limb muscles, not including the hand, shows that the humerus lacks muscles on its flexor surface, and that the only direct flexor of the forearm is the coracoradialis, acting by way of its tendon. The muscle itself is located deep on the pectoral girdle, internal to the two supracoracoidei, and covers the coracoid fenestra ventrally. Its fibers originate on the medial, cartilaginous part of the coracoid, and converge to the tendon, which then runs in its groove on the humerus and terminates at the point marked by a dot on the radio-ulna, in Fig. 10.

The greatly enlarged flexor carpi radialis superficialis and extensor carpi radialis (on dorsal aspect of forearm) are actually more important as indirect flexors of the forearm than in the functions indicated by their names, and obviously much more powerful than the coracoradialis, at least in the male. Their development is no doubt responsible for the two distal crests of the humerus already described. That this circumstance is not limited to Centrolenids and certain big-armed Hylids is shown by Ritland's (1955, p. 239) remarks on *Ascaphus* (he uses the term "antibrachial flexors" for the enlarged forearm muscles): "Mature male *Ascaphus* have tremendously enlarged forearms, primarily a result of the striking expansion of the antibrachial flexors and correlated development of broad distal wings (cristae) on the humerus for their origin. . . . The muscles of females and immature have exactly the same relative positions as those of fully grown males, but they are smaller, and since distal cristae are lacking, all originate from the humerus proper."

In the female of *Centrolene* the only differences seen in the shoulder and arm were: (1) absence of the spine and distal crests on the humerus; (2) from the ventral side, the more lateral part of the deltoid (acromiohumeralis) could be seen uninterruptedly as it went to its insertion on the shaft of the humerus; (3) the edge of the anconeus was likewise visible without interruption on its way to the proximal end of the radioulna; (4) the two "anti-

brachial flexors" were each no wider than the palmaris longus, although the forearm still appeared conspicuously bigger than the upper arm.

Jones (1933) gives a ventral view of the pectoral muscles of *Hyla arborea;* they are like those in the female of *Centrolene.*

Figures 18-20 are intended for comparison with Noble's (1922) illustrations of thigh muscles and their tendons in Salientia. Although he does not show any Hylids or Centrolenids, he lists 21 species of *Hyla,* 5 of *Phyllomedusa,* one each of *Agalychnis* and *Pternohyla, Centrolene geckoideum* and *Centrolenella* (now *Centrolene*) *antioquiensis,* among many others, as having the "typical bufonid tendon complex" on the ventral aspect of the knee; this is characteristic of his suborder Procoela (Bufonidae, Brachcephalidae, Hylidae, plus the recently separated Centrolenidae). The semitendinosus tendon receives on its upper edge, just before its insertion, the sartorius; the gracilis passes internally to these but at its insertion is combined with them. I have compared the thigh muscles and their tendons in *Centrolene prosoblepon* with those of *Hyla alleei* and find them so much alike that the same illustration would almost serve for both, even though among the various genera which have the "bufonid complex" there are many minor differences of detail. This, then, is to be added to the numerous features in which Centrolenidae appear directly related to *Hyla.*

CONCLUSIONS

It seems evident, in comparing the known Centrolenids with one another, that the primitive stock of this family had the following combination of characters:

(a) *Those not present in Hyla.* (1) Partial fusion of tibiale and fibulare; (2) basal pad in the palm; (3) T-shaped terminal phalanges.

(b) *Those present in some Neotropical species of Hyla.* (1) Eyes large and directed about 45° forward; (2) vomerine teeth present; (3) dorsal color green, with ample pigment, and capable of turning purplish in alcohol; (4) forearm in both sexes relatively large, with distal crests on the humerus but not a lateral spine in the male; (5) a posterior crest on the femur.

(c) *Those present in Hylidae and allied families.* (1) Procoelous vertebrae; (2) arciferal pectoral girdle; (3) characters of pectoral and thigh muscles; (4) intercalary cartilages in digits, etc.

As *Centrolene* is undoubtedly specialized in the addition of a

humeral spine in the male, and *Teratohyla* in the prepollical horn, this stem-form of Centrolenidae would be a species of *Cochranella*.

The fusion of tibiale and fibulare appears to be the major specialization setting off the Centrolenids, yet it is not actually a radical change, since the two bones are easily distinguishable in *Centrolene* for most of their length. The pad on the hand and the T-shaped phalanges appear to be specializations of minor importance, occurring here independently of their development in other families. These conclusions should be qualified by the statement that the writer has not examined the anatomy of other families of arboreal frogs, such as Hyperoliidae and Rhacophoridae.

Explanation of labelling:

Roman numerals indicate foramina for cranial nerves as numbered.

ach—acromiohumeralis (deltoid)
am—adductor magnus
anc—anconeus
ang—angular
ar—arytenoid cartilage
$c_{1,2,3,4}$—centrale 1-4
cb—coracobrachialis
clav—clavicle
elei—cleithrum
$co_{1,2}$—cornua 1, 2 of hyoid
cor—coracoid
crt—coracoradialis tendon
d—dentary
$dc_{2,3,4}$—distal carpals 2-4
e—ethmoid
ecb—extensor cruris brevis
eo—external oblique
eno—endochondral ossification
eph—episternohumeralis (deltoid)
f—fenestra
fcrs—flexor carpi radialis superficialis
fcu—flexor carpi ulnaris
fib—fibulare (calcaneum)
fp—frontoparietal
gm—gluteus magnus
gr—gracilis
hy—body of hyoid
i—intermedium
if—ischioflexorius
mm—mentomeckelian bone
mx—maxillary
n—internal naris
na—nasal
N. p.—peroneal nerve
N. t.—tibial nerve
op—foramen for deep ophthalmic nerve
p—palatine
pab—pectoralis abdominalis
pal—palmaris longus
pec—pectineus
per—peroneus
pll—plantaris longus
pm—premaxillary
pp—prepollex
ps—parasphenoid
pst—pectoralis sternalis
pt—pterygoid
q—quadrate
qj—quadratojugal
r—radiale
ra—rectus abdominis
r-u—radio-ulna
s—sternum
sa—sartorius
sc—scapula
scs—subcoracoscapularis
smb—semimembranosus
smt—semitendinosus
sq—squamosal
spcp—supracoracoideus profundus
spcs—supracoracoideus superficialis
st—stapes (columella)
tal—tibialis anticus longus
th—thyroid cartilage
tib—tibiale (astragalus)
tp—tibialis posticus
u—ulnare

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Observations on the Behavior of Brasilian Halictid Bees, III [1]

BY

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ABSTRACT: This paper presents data on the nests of several Brasilian halictine bees, as follows: *Neocorynura polybioides* (Ducke), *Pseudaugochlora nigromarginata* (Spinola), *Megommation insigne* (Smith), *Augochlora semiramis* (Schrottky) and *morrae* Strand, *Augochlorella michaelis* (Vachal), *Paroxystoglossa andromache* (Schrottky), *Habralictus canaliculatus* Moure, and *Caenaugochlora curticeps* (Vachal). Virtually all the data were collected on the Southern Brasilian plateau, in the State of Paraná.

Several of these species exhibit incipient stages in the establishment of social behavior, as discussed in the Conclusions.

INTRODUCTION

This paper consists of fragmentary, but we believe significant, observations mostly on nesting behavior of various halictid bees. The observations were made on the southern plateau of Brasil, in the state of Paraná, except as otherwise noted. The altitude of this area is about 900 meters; some general features of its climate are noted by Michener, Lange, Bigarella and Salamuni (1958) in connection with data on bee nesting sites in the Bariguí roadside banks near Curitiba.

1. Part I on *Pseudagapostemon*, Ann. Ent. Soc. Amer., vol. 51, 1958, pp. 155-164. Part II, on *Paroxystoglossa jocasta*, Jour. Kansas Ent. Soc., vol. 31, 1958, pp. 129-138.

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2. Department of Entomology, University of Kansas, Lawrence, Kansas, U. S. A. Field work for this author's part in the study was made possible thanks to a John Simon Guggenheim Memorial Foundation Fellowship and aid kindly made available by the Campanha Nacional de Aperfeiçoamento de Pessoal de Nível Superior, Rio de Janeiro; the Conselho Nacional de Pesquisas, Rio de Janeiro; and the Rockefeller Foundation, New York. In particular, thanks are due to Father J. S. Moure for the use of facilities of the Secção de Zoologia, Faculdade de Filosofia, Universidade do Paraná, Curitiba, Paraná, Brasil.

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The methods of study used include several of those listed by Michener, Cross, Daly, Rettenmeyer and Wille (1955). Ordinarily nests were opened on cold days or at a time of day when all the occupants were presumed to be inside. If this were impractical or if there were time to obtain information on the activities of the various individuals inhabiting a nest, the nest was watched for one or more hours before opening it, and the pollen collectors (or bees exhibiting other behavior) were captured as they returned to the nest and separately preserved. Subsequently, dissections and measurements revealed whether such bees differed in ovary size, fertilization (shown by presence of sperm cells in the spermatheca), age or previous activities (shown by mandibular and wing wear), and size (as indicated by measurements of wing length) from bees found in the nest or exhibiting different behavior. Ovaries were classified in the following categories: very slender, slender, slightly enlarged, enlarged, and much enlarged. Each ovary has three ovarioles in halictine bees, and in the species discussed in the present paper, enlargement of the ovaries usually involved all or most of the six ovarioles. (This is in contrast to some workers in *Lasioglossum* where one ovariole, or one in each ovary, may become enlarged while the others remain very slender.)

Some presumably generic differences in the ovaries were noted, as follows: In *Paroxystoglossa andromache* (Schrottky), *jocasta* (Schrottky), *seabrai* Moure and *spiloptera* Moure, the anterior parts of the ovaries, where the ovarioles are small, have the ovarioles arranged in the same horizontal plane so that all of the ovarioles are visible in this region in dorsal or ventral view. The same is, to a lesser degree, true of *Pseudaugochlora nigromarginata* (Spinola). In other genera studied the three ovarioles of each ovary are crowded together so that if seen in section they form a roughly triangular figure. Also, in some genera, such as *Paroxystoglossa* and *Pseudaugochlora*, oocytes of moderate size occur anterior to the large oocytes that are nearing the size for laying. The result is rather long ovaries, a mature oocyte being not a great deal over half of the total length of the ovary (figure 1). In some other genera (e. g., *Neocorynura*), the oocytes anterior to the large posterior ones are small, so that the ovarioles seem to consist largely of one oocyte each, which is much more than half of the total ovary length (figure 2).

Mandibles were classified in the following categories: unworn, slightly worn, well worn, much worn, very much worn.

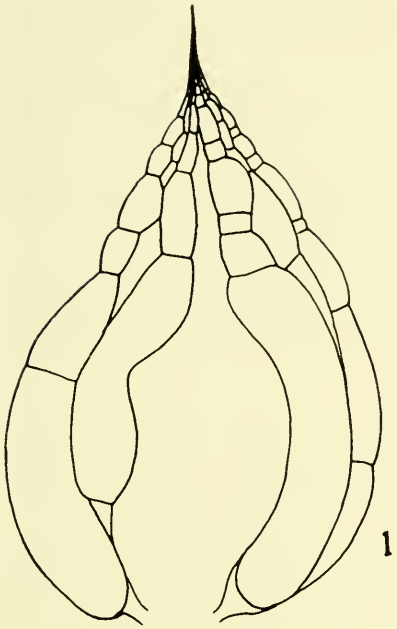

FIG. 1. Ovaries of egg laying female of *Pseudaugochlora nigromarginata.*
FIG. 2. Ovaries of egg laying female of *Neocorynura polybioides.*

Neocorynura polybioides (Ducke)

Seasonal Cycle: Females of this species appear early in the spring. A few were taken on flowers near Curitiba on August 30, 1955 and on October 1 a single female was seen flying about one of the Bariguí roadside banks. Males were first seen on December 14, when both sexes were found abundantly on flowers at Xaxim, a suburb of Curitiba.

Nests of this species were found on December 21, 1955, in the Bariguí roadside banks, in a vertical bank of decomposed gneiss, at a point where it overhangs and is therefore shaded. On this date four nests were opened. Several freshly opened cells, with feces, were found, indicating recent emergence of adults. One male and one female were found in their cells, not yet emerged. Three male and five female pupae were found, and one mature larva. No younger stages were found. One unmated, unworn (young) adult female was taken flying along the bank.

On January 3, 1956, a bee was found constructing a new nest in the same vicinity. This does not mean that there was synchronization of establishment of new nests and abandonment of old ones

at this time, however, for two nests opened in similar banks at Araucaria, Paraná, on January 13, 1956, were old nests containing half grown larvae, male and female pupae, and adults of both sexes ready to emerge from the cells. A nest from the Bariguí roadside banks opened on January 25 contained a half grown larva, four prepupae, three female and one male pupae, and an open cell apparently ready to be provisioned. Finally, a nest opened on March 11 contained one female and three male pupae.

From these data it would appear likely that this species passes the winter as fertilized females which emerge as early as the end of August, that their progeny reach maturity by mid-December, and that from that time until fall (March) new adults are produced more or less continually.

Social organization: Females, with worn mandibles or wings, but with slender ovaries and empty spermathecae, were not found. Therefore we judge that there is no worker caste nor approach to it. However *Neocorynura polybioides* is not an entirely solitary bee. One nest opened on December 21 contained two fertilized females with enlarged ovaries in approximately egg-laying condition (largest oocytes 1.3 and 1.9 mm. long) and with the crops full of pollen. Their mandibles were slightly worn, and we judge these to be bees that had overwintered and provisioned the twelve cells of the nest. Their progeny were emerging and one young unfertilized female was also in the nest. Although the youngest bee was a mature larva, it seems likely that the old bees would soon have resumed reproductive activity. Another nest opened on the same day also contained two fertilized females with somewhat enlarged ovaries (longest oocytes .6 mm.) but with unworn mandibles. We do not know whether they had overwintered and produced the brood emerging at this time; possibly the mother or mothers had died and these were among the progeny. A young unfertilized female was also in the nest, as was a female parasitized by a strepsipteran.

Although evidence such as that mentioned above indicates that at least two egg-laying bees may occupy one nest (and cell cluster) simultaneously, it is also apparent that a single bee may construct a nest. On January 3, 1956, one female was found building a nest; she had constructed a chamber but as yet no cells. A nest with three empty cells that had never been occupied and only four occupied cells, all containing pupae or adults ready to emerge, was found on January 13, suggesting that a single bee made the nest and that she died before we opened it. On January 25 a single female

was found in a nest containing pupae; she was mated and had much enlarged ovaries (largest oocyte 1.5 mm. long) but her mandibles were not or scarcely worn. We judge that the parental bee or bees had died and that this was one of their progeny nearly ready to start egg laying. On February 21 a fertilized female with much tattered wings, very much worn mandibles, and ovaries moderately enlarged and yellowish (longest oocyte, or chamber, .5 mm.) was found flying along the bank as though lost. Unpublished work on North American halictids has shown that senile bees often behave in this way and we judge that this may have been an overwintering bee nearing the end of its life.

Nests: Both at the Bariguí roadside banks and at Araucaria nests of this species were mostly in loose groups, several in one or two square meters (see Michener, Lange, Bigarella and Salamuni, 1958). Each nest consists of a burrow about 3 mm. in diameter, slightly constricted at the entrance, extending horizontally or sometimes slanting upward or downward into the bank of decomposed gneiss. At a distance of 2.5 to 9.5 cm. from the entrance, the burrow opens into a chamber, which is not especially smoothed on the inside. The chamber is rather irregular in shape, generally larger in horizontal diameters (up to 3.5 cm.) than in height (up to 2.7 cm.). There is no burrow extending on into the bank from the chamber.

Within the chamber is an earthen cell cluster sometimes supported by a single large central pillar (fig. 34); more often supported by three to five relatively slender pillars extending from the floor of the chamber to the under side of the cell cluster (fig. 34). Horizontal dimensions of the irregularly shaped and slightly rough cell clusters range from 1.8 to 2.7 cm., while vertical dimensions range from 1.2 to 1.7 cm.

Apparently completed clusters contain from 7 to 13 cells. Very inconclusive evidence suggests that a single female might produce as many as 7 cells while two females working jointly might produce 13 or so. The cells are usually nearly vertical but most clusters contain one or more slanting or even nearly horizontal cells. The walls around the cells and the earth of the cluster between cells is rather thick, in contrast to *Paroxystoglossa* and some others.

The cells are flatter on one side than the other, as usual in halictines. In slanting or horizontal cells the flatter side is lowermost, the more concave side uppermost. Vertical cells have the same shape. The pollen ball is placed near the lower end of the

flatter side, as in other halictines. The mature larva deposits feces on the more convex surface near the lower end of the cell (fig. 3.). The cells range from 9 to 10.5 mm. in length (from the surface of the cell cluster at the cell opening), 4.5 to 5 mm. in greatest diameter, with the opening 3 to 4 mm. in diameter. They are lined with a waxlike material except in the neck region.

We have little data on the manner of nest construction. The one nest excavated that was obviously being built had a small chamber (1 cm. in diameter) with a large mass of soft dirt resting on the center of the chamber floor. From this we assume that as the chamber is dug, some of the dirt from it is left in the center of the chamber and later formed into the firm cell cluster with its cells,

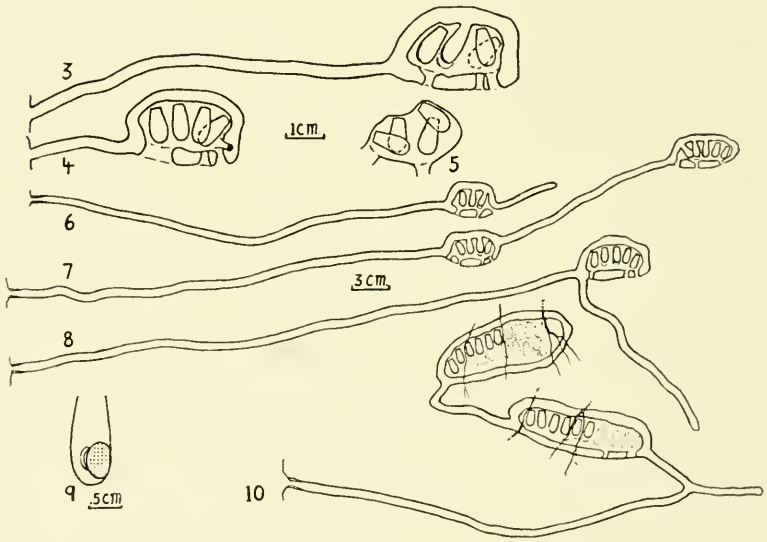

FIG. 3. Diagram of nest of *Neocorynura polybioides*. Heavy lines indicate deposition of fecal material in two cells. The open cell has been used twice.

FIG. 4. Diagram of nest of *Neocorynura polybioides*, showing a different cell arrangement. One supporting pillar of the cell cluster, which is more or less horizontal, is broken; the broken surface is shown as black.

FIG. 5. Diagram of cell cluster of nest of *Neocorynura polybioides*, showing an unusually irregular arrangement of cells.

FIGS. 6, 7, 8. Diagrams of nests of *Pseudaugochlora nigromarginata*. Some of the cells have been used twice. Cell clusters are of only moderate size.

FIG. 9. Diagram of unusual nest of *Pseudaugochlora nigromarginata*, showing large cell clusters. The upper cluster has been much thickened by repeated use; both cell clusters have inactive regions, shown by earthfilled cells. The cell clusters are largely or entirely supported by roots.

FIG. 10. Sectional view of cell with pollen ball and egg.

supporting pillars, etc. Cells may be reused at least twice (fig. 34). When this happens considerable soil is placed in the bottom of the cell before it is reformed and lined. Obviously the height of the cell cluster (and probably of the chamber) must be increased at the same time.

An interesting nest found on December 21, 1955 was being made by an unworn stylopized bee. Possibly it was quite abnormal. It contained a small mass of very soft, friable soil, in which was a single cell lined with waxlike material (fig. 34).

Lüderwaldt (1911) described the nests of another *Neocorynura*, *N. erinnys* Schrottky. They were in rotting wood, the cells closely clustered and rectangular in section, and in other ways also so different from those of *N. polybioides* as to make one wonder if Lüderwaldt's description applies to bees of the same genus as *N. polybioides.*

Pseudaugochlora nigromarginata (Spinola)

Seasonal Cycle: Observations were begun on this species on September 29, 1955, when a single nest was found in a Bariguí roadside bank and opened. It contained numerous open old cells, and one closed with a pollen ball and egg. We presume that females that had overwintered were at this time provisioning newly refurbished cells in old nests. The next occupied nest of this species was found in the same vicinity on November 22. It contained two female pupae, no other immature stages, perhaps because five cells were moldy. On February 2 a male was found in a burrow 10 cm. deep in a bank near Curitiba. (At Fazenda São José, Guaranesia, Minas Gerais, Dr. Domiciano P. de Souza Dias of Piracicaba, São Paulo, found a male in a short burrow in a bank on June 19, 1946. This is an area of milder winters than Curitiba.) Nests found in banks near São José dos Pinhais, Paraná, on February 21, 1956, contained cells being provisioned, cells with eggs, and in the same nests, prepupae and pupae of both sexes. We do not know whether the absence of feeding larval stages in the few cells examined was a happenstance or a significant fact. Females were observed on flowers collecting pollen as late in the fall as March 24 and visiting flowers for nectar on June 28, a warm winter day.

The fact that this species flies on warm days in winter suggests that it is active whenever temperatures are suitable and that winter may not cause a basic break in the life cycle as it does in many bees

typical of the southern Brasilian plateau. *P. nigromarginata* is basically tropical and it or close relatives range to Mexico and southernmost Texas. The well worn mandibles and much tattered wings of the fertilized egg-laying female that had evidently recently started her spring egg laying when the nest was dug on September 29 indicate that she must have been active also the preceding summer or autumn. The individual taken on flowers on June 28 was fresh, unworn, and unfertilized. If winter does not kill all but one age group, it will not have the synchronizing influence that it has for many bees and it is not surprising to find bees in various stages throughout the warmer part of the year. It appears certain, however, that reproduction ceases during the winter months in the vicinity of Curitiba. Bertoni (1911) states that this species passes the winter as adults in the nests and reported three individuals in a single nest.

Social organization: Our data is entirely too meager to give a clear picture of the social behavior of this bee. Several times we noticed a female plugging the nest entrance with her head, as did Ihering (1904), but we do not know whether such guarding occurs principally in nests with more than one bee or whether the guard will turn and plug the entrance with her abdomen, as do most halictines.

The nest opened on September 29 contained three females, all fertilized, only one of which was in egg-laying condition (all ovarioles enlarged, longest oocyte 2.6 mm.). The two with slender ovaries (longest oocyte .7 mm.) each contained a conopid larva among the abdominal organs so that they cannot be considered as normal. The nest opened on November 22 contained but one female; she was fertilized and had large ovaries (all ovarioles enlarged, longest oocyte 1.9 mm.). Although her nest was old, containing abandoned earth-filled cells probably used the previous season, it contained but seven cells used during the spring of 1955; possibly this is a normal number for a lone female to prepare and provision. An old nest opened on February 3 contained no immature stages; the single adult bee was an unworn unfertilized female with feebly enlarged ovaries.

On February 21 one old nest was found to contain a fertilized female, rather fresh, that was apparently constructing a new cell in the earth of the old cell cluster. On the same day another nest was found containing three females. One was a fertilized egg-laying individual (all ovarioles enlarged, longest oocyte 2.7 mm.)

showing slightly worn mandibles and wings. A second was also fertilized but unworn and with very slender ovaries (longest oocyte .8 mm.); probably it was young and a daughter of this nest. The third individual was workerlike in that, although its mandibles were well worn and its wings showed several nicks torn from the margins, indicating moderate age and considerable activity, it was not fertilized and its ovaries were very slender (longest oocyte .5 mm.). This is the individual that was carrying pollen into the nest. Neither of the fertilized ones was seen outside the nest in an hour of observation before we opened it. A third nest opened on the same day contained two females, one an only slightly worn but unfertilized individual with slender ovaries, probably workerlike; the other a not or slightly worn egg layer, fertilized, with large ovaries.

From February 26 to March 4 seven females were taken on flowers of *Cassia* in Curitiba while actively collecting pollen loads. Of these one was workerlike in being unfertilized and having slender ovaries in spite of well worn wings and mandibles. Three had large ovaries, and were fertilized; all three were but little worn. The remaining three were also but little worn; two were unfertilized, one of them with one oocyte in one ovary much enlarged (2 mm. long) but the ovaries otherwise slender, the other with the ovaries slender; the third was fertilized with slender ovaries.

It is possible to say from these data that the egg-laying individuals often collect pollen and presumably do the entire work of nest construction and provisioning. This may happen at any time during the season of activity of this bee. However, it is also apparent that some individuals (probably a minority) work extensively while not fertilized and probably never do mate or lay eggs. Such individuals have been found only after midsummer and may be absent in spring and early summer. These workerlike females occur in nests with egg layers and do some (or all) of the foraging.

There is a suggestion that an average size difference exists between egg layers and the workerlike individuals. Wing lengths of eight clearly egg-laying bees ranged from 7.8 to 8.8 mm. with a mean of 8.3 mm. while those of four obviously workerlike individuals ranged from 7.6 to 7.8 mm. with a mean of 7.7 mm. Individuals intermediate as to ovary development were found; from the enlargement of only one or two ovarioles we judge these individuals to be actually intermediate and not merely young which would later develop large oocytes in all ovarioles, but we cannot be certain of this.

Nests: The nests are found singly or in groups of three or four in vertical banks of soil; those which we found were in decomposed gneiss or basalt. The distribution and exposure of those in the Bariguí roadside banks is shown by Michener, Lange, Bigarella and Salamuni (1958). The nests are often high in banks, so that it may be difficult to open them.

At the entrance the burrow is constricted to about 4 mm. in diameter by material obviously transported from elsewhere in the nest by bees. Sometimes the entrance is located in the center of a conical depression as much as a centimeter in diameter. This depression is often circularly scratched, perhaps by the mandibles. The diameter of the burrow ranges from 6.5 to 8 mm. The burrow is usually unbranched and extends into the bank. It may be rather straight or sinuous, and often slopes upward, sometimes downward. Figures 6 to 9 illustrate some of the patterns which we have seen. At a depth of 14 to 48 cm. (average of eight, 34.1 cm.), the burrow opens into a large cavity or chamber. Horizontal diameters of the chamber in apparently completed nests range from 4.3 by 3.4 cm., in the case of a small chamber, to 10.5 by 6.0 cm. in the case of the largest chamber we found. Vertical heights of chambers vary from 2.7 to 4.7 cm. The chamber is irregular in shape, not particularly smooth walled. Most of the nests which we opened contained only a single chamber and had no burrow leading on from the chamber. However, several had such a burrow, connecting to almost any part of the chamber, and in two cases it lead on to a second chamber (figs. 7 and 9). Ihering (1904) described (under the name *Augochlora gramminea* Smith) a nest in which there were four chambers connected in sequence. He considered the cell clusters farthest from the surface to be the newest because of their smaller size and less regular shape.

In the chamber is a large earthen cell cluster supported by fairly robust pillars of earth. The number of pillars ranges from three to seven or eight. They are generally between the bottom of the cell cluster and the floor of the chamber, but in one nest a very large pillar connected the top of the cell cluster with the roof of the chamber (fig. 36). The distance between the wall of the cluster and that of the chamber is 6 or 7 mm.

Within the cell cluster the cells are in a generally vertical position. Their openings are rather widely separated, 5 to 8 or more mm. apart, the axes of the cells in general converging below. Cells do not usually closely approach one another nor the lower surface of

the cell cluster. This is in striking contrast to nests of such forms as *Paroxystoglossa jocasta* (Schrottky) (see Michener and Lange, 1958a) which are noteworthy for the thin walls between and around the cells, which diverge slightly from their openings.

The manner of construction of the cell cluster is unknown. However, one nest, excavated on November 24, 1955, contained a chamber 3 cm. long, in the center of which was a mass of soil so delicate that it fell apart at a touch. It certainly contained no wax-lined cells, and it is not clear whether it was supported by pillars or rested on the floor of the cavity. By analogy with *Paroxystoglossa* (Michener and Lange, 1958a) it seems probable that the cell cluster is built of friable soil probably removed from the walls of the chamber as it is enlarged and that only later does the cluster become firm. The nest mentioned above was inhabited and doubtless being built by a single female. She was an old bee, with wing margins entirely worn away and mandibles well worn. She had been fertilized and had large ovaries, but the longest oocyte was only 1.7 mm. long, not nearly large enough to be laid. The possibility exists that she was senile and her behavior abnormal, although the condition of the ovaries does not support this idea.

As already indicated, the size of the cell cluster is highly variable. It is not surprising that the number of cells in it is also variable. We have seen apparently completed clusters with from 7 to 43 cells (average number of cells in nine clusters, 15.5). The larger clusters often have occupied cells in only one area, *e. g.*, one end or much of the lateral margin, the rest of the cluster containing old, empty or earth filled cells which had once been used (fig. 9). The largest number of occupied cells that we found in any cluster was 22 in a nest opened on February 21; this cluster also contained 21 open cells, all old and empty except for one which was being provisioned. The nest was occupied by three bees when it was opened; one was a fertilized egg layer, one an unfertilized worker-like individual, and the third a fertilized but unworn, probably young individual.

Although the impression given by the distribution of abandoned and used cells in large clusters is one of cluster (hence chamber) growth during the seasons or years of occupancy, leaving sections of the cluster abandoned, the bees do re-use old portions of the cluster. It is common to find cells that have been used two or three times. In such cases some dirt is placed in the cell and the new wax lining is thus separated, at the base of the cell, by .5 to 5

or 6 mm. of soil from the old lining (figs. 6 to 8, 10, 35, and 36). The result is that new cells are at somewhat higher levels than those they replace, and hence the cell cluster becomes thicker as it is reused. Obviously the height of the chamber must be increased also.

The cells are lined with waxlike material except near the openings. Their length varies from 13 to 15 mm; maximum diameter, 6 to 7 mm; diameter of cell opening or neck, 4 to 4.5 mm. They are flatter on one side than the other, the flatter side corresponding to the lower surface of horizontal cells. The pollen ball is placed against the flatter side of the cell, near the lower end of the cell (fig. 9). The pollen ball is about 5 mm. in maximum diameter, little if any over 3 mm. in thickness. The curved white egg, 2.8 to 3 mm. long, lies on the free side of the pollen ball, in contact with it at both ends. The egg tapers distinctly posteriorly; near the anterior end it is .7 to .8 mm. in diameter while near the posterior end it is .5 to .6 mm. in diameter.

Megommation insigne (Smith)

Seasonal cycle: So few nests of this crepuscular or nocturnal species were opened that we can contribute practically nothing concerning the seasonal cycle. The nests were found in the packed soil of small paths through grassy or weedy areas of nearly level ground near forested areas in the vicinity of the Barigui roadside banks, Curitiba, Paraná. Jörgensen (1912) published a fairly extensive account of this species, which should be consulted for further information.

A nest opened on December 16, 1955, contained an adult female and, in the cells, two female pupae. A nest opened on January 5, 1956, contained two adult females and, in the cells, eggs, young larvae, and pupae. A nest opened on February 16 contained four adult females and, in the cells, eggs. A nest opened on May 4 contained two adult females, but the cells were entirely empty.

Social organization: From the above, it is obvious that more than one female may occupy a single nest. Of the two females in the nest opened January 5, one was fertilized and had large ovaries (longest oocyte 3.5 mm. long) while the other, which was unfertilized, had small slender ovaries, with the longest oocyte .6 mm. long. Both had slightly worn mandibles, the unfertilized one if anything showing more wear than the other.

Among the four females removed from the nest which was opened on February 16, one, which had been fertilized, had well-worn mandibles, a few nicks in the wing margins, and enlarged ovaries (although the longest oocyte was only 2 mm. long). Evidently this was the egg layer. The other three, all unfertilized, had unworn or slightly worn mandibles, undamaged wings, and slender ovaries with the longest oocyte .5 to .8 mm. in length.

To judge by these two nests, there must be workerlike individuals and egg layers, much as in *Pseudaugochlora nigromarginata.* Measurements of wing lengths of two egg layers were 10.1 and 11.0 mm.; of four probably workerlike bees, 9.5, 9.8, 10.1, and 10.2 mm.

Of the two bees which may have been preparing to pass the winter when their nest was opened on May 4, one was unworn and unfertilized, the other had much worn mandibles and wings and was probably also unfertilized.

Nest structure: This bee is especially remarkable for its beautiful nests, earlier described under the name *Megalopta ipomoeae* Schrottky by Jörgensen (1912) and Bertoni (1918). At the entrance, each nest opening is guarded by an erect turret made of soil. In bare places the turret is usually relatively low (fig. 37), 10 to 13 mm. in height, but in a grassy place a turret which reached nearly to the tops of the grass blades was 47 mm. high. The inside diameter of the turret is about 7 mm.; its walls range up to about 5 mm. in thickness.

The burrow below the ground surface enlarges to about 9 mm. in diameter. It descends straight or in sweeping curves to a depth of 31 to 42 cm. below the ground surface. At a depth of 17 to 30 cm. from the surface, a lateral burrow extends horizontally or usually slightly upward to a large, uniformly shaped, subspherical chamber which measures 5 to 6 cm. in any diameter (fig. 11). The inside surfaces of the burrows are beautifully smooth. They have no wax lining but are so smooth that a careful examination had to be made to be certain that there was no lining. The chamber is also very smooth, but one can see the marks of the mandibles on its walls, unlike the walls of the burrows.

The chamber contains a cell cluster, the entire surface of which is smooth and polished, but not covered with waxlike material. The cell cluster is 28 to 32 mm. long, about 24 mm. wide, and 24 or 25 mm. in height. It is supported well above the floor of the chamber

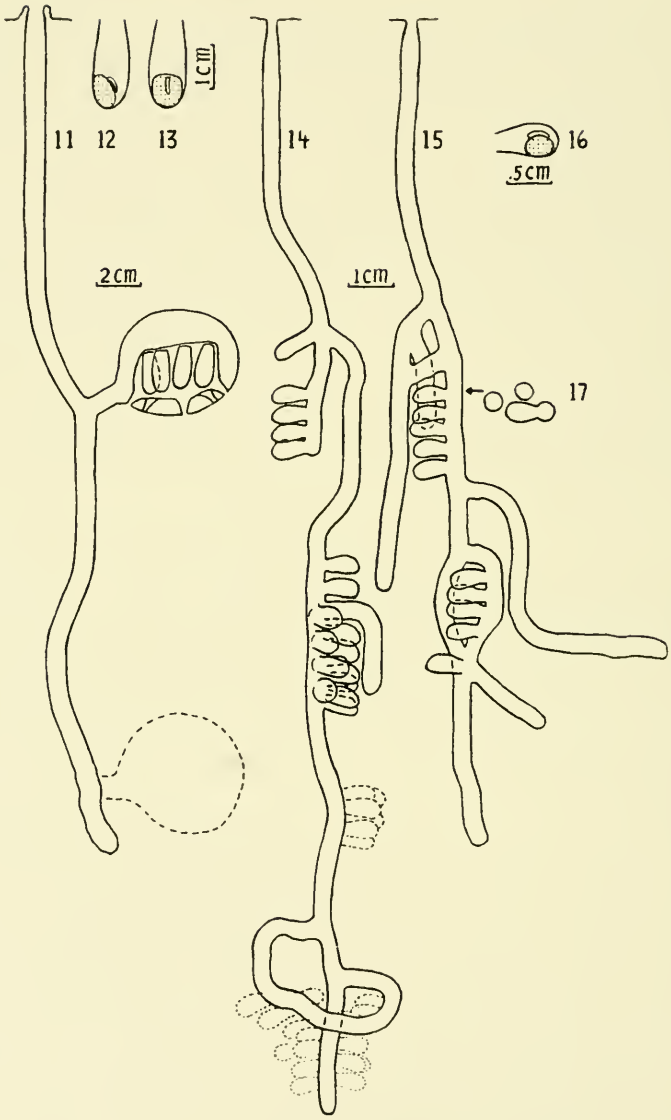

FIG. 11. Diagram of nest of *Megommation insigne*. Broken line near bottom shows position of abandoned, earth filled chamber.

FIGS. 12, 13. Sectional views of cell, showing pollen mass and egg.

FIGS. 14, 15. Diagrams of nests of *Augochlora semiramis* (October 25, 1955). Dotted cells in 14 are old and earth filled.

FIG. 16. Longitudinal section of cell of *Augochlora semiramis*, showing pollen mass and egg.

FIG. 17. Cross-section of nest shown in figure 15 at level indicated by arrow showing how vertical branch burrows pass close to a cell.

by four to seven pillars which are thick where attached to the cell cluster and taper to small diameters (1.5 to 4 mm.) where they attach to the floor of the chamber. The pillars extend downward from the cluster or more or less outward from its lower outer margins so that some of them can be seen from above [see especially Jörgensen's (1912) illustration]. They support the cluster at such a height that its flattened upper surface is 32 to 34 mm. above the floor of the chamber. The upper surface of the cluster slopes downward toward the main burrow of the nest. The measurements given above, as well as figure 11, show the unusual amount of space around, and especially above, the cluster.

The cells are vertical or nearly so, opening on the upper surface of the cluster. They vary from 18 to 20.5 long, 7.5 to 9.5 mm. in maximum diameter, with the entrances 5 to 5.3 mm. in diameter. Only about the lower half of each cell is waxed. The walls of the cluster beneath and lateral to the cells are about 1 mm. thick and convexities indicating the lower ends of the cells on the under surface of the cluster are not or scarcely visible. As usual in halictines, each cell has one side flatter than the others (fig. 12), and the pollen mass is placed near the bottom of the flatter side. It is quite soft and there may be a little liquid in the bottom of the cell. The pollen mass is about 7.5 mm. long (vertically), 6.8 mm. wide, and 4 mm. thick. It is slightly rectangular, seen from the side on which the egg is placed (fig. 13), and looks as though it had slumped down a little in the cell.

The egg is placed on the exposed subvertical surface of the pollen mass. It is white, 3.8 mm. long, arcuate, .85 to .90 mm. in maximum diameter near the anterior (upper) end, .8 mm. in diameter near the posterior end.

One nest had remnants of an old cluster, now abandoned and largely earth filled, below the level of the occupied cluster (fig. 11). This would indicate long continued use of the same burrow.

Augochlora semiramis (Schrottky)

This bee is extremely common, at least at some seasons of the year, in cleared and savanna areas near Curitiba, Paraná. Females were common on flowers of *Senecio trichocaulon* in the savanna near the suburb of Xaxim, Curitiba, in October, 1955. In December it was noted that they were much less common in the area, but were gathering pollen.

Twelve females taken on flowers of *Senecio* on October 9 all had slender to very slender ovaries and unworn or scarcely worn

mandibles and wings; all but one had been fertilized. Three of the twelve were collecting pollen loads on the scopa when they were captured. From this we suppose that young adult fertilized females survive the winter and start their nesting activities in the spring (October). The only nests opened were found on October 25. The three nests which we opened on that day had one, three, and eight bees (females) in them. These twelve bees all had not or but little worn mandibles and wings and had been fertilized. One bee in each nest had slightly to considerably enlarged ovaries; the others had slender to very slender ovaries. The ones with large ovaries were not the largest of the bees. These meager data show that several bees may occupy a nest, that bees with slender ovaries may collect pollen, but that such bees are not workerlike in the sense of being unfertilized or smaller than the egglaying individual. The social organization, so far as we know it, seemingly resembles that of *Augochloropsis sparsilis* (Vachal), to be described in a subsequent part of this series of papers. Workers may, however, appear later in the year.

The nests, opened on October 25, 1955, were vertical or slanting burrows in firm bare level ground. They were widely scattered, there being no evidence of gregariousness. The diameter of the opening was about 2 mm. and of the burrow elsewhere, about 4 mm. The burrows were unbranched to a depth of four to eight centimeters, below which there were several branches (figs. 14 and 15). Cells were located in groups of 5 to 11 or more, about as close as they could be placed, along the vertical main burrow, or on a branch. The axes of the cells are approximately horizontal. The cells do not project in all directions from the main burrow, but extend toward one quarter or another forming a vertical series. Commonly one to several of the branch burrows pass vertically close to the group of cells, often meeting one another to form complete rings, so that in some cases (not shown in the figures) the group of cells becomes rather well isolated from the surrounding soil. Since the cells are close together and their walls are built by the bees of very thin soil, the group of cells is very delicate. It cannot be removed intact, but can be removed in fragments from the surrounding soil, which then shows a series of concavities corresponding to the cells.

Many of the cells were old and earth filled, showing that the nests had been occupied at least the season before. However, cells being constructed, others being provisioned, and others containing

eggs, small larvae, and half grown larvae were found. Most of these cells constituted new or completely reconstructed groups but some were among groups of old cells of the previous season.

The cells are about 7 mm. long, 4 mm. or slightly less in greatest diameter, with the diameter of the entrance about 2.2 mm. They are lined with waxlike material. The lower surface is flatter than the upper (fig. 16). The pollen ball is considerably flattened, the horizontal diameters being 3.1 to 3.4 mm.; the vertical diameter 2.0 to 2.4 mm. The arcuate egg is placed on top of the pollen ball, parallel to the long axis of the cell as in other halictines. It is white, 2.1 to 2.3 mm. long, .52 to .56 mm. wide, only slightly thinner posteriorly than anteriorly.

Augochlora morrae Strand

Two nests of this species, as well as a male in a different burrow, were found in a vertical bank near São José dos Pinhais, Paraná, on February 21, 1956. In the nests roughed out but unlined cells, waxed cells ready for use, as well as small larvae and a white female pupa were found. Thus individuals in all stages could be expected at this season (late summer). Outside the region of the southern Brasilian plateau, we have data on one nest in a roadside bank between Boa Vista and Corcovado, Rio de Janeiro, opened February 25, 1956, by Dr. Carlos Alberto Campos Seabra and Father J. S. Moure. This nest contained a prepupa, eight female pupae, and two male pupae. A nest was excavated by us at about sea level in flat ground at Guaruva, Santa Catarina, on October 30, 1955. The burrow was closed at the surface; we found it by chance. A single female was in the nest. There were eight cells, those nearest the surface containing pupae (one male, one female), the rest containing larvae of various sizes, the smallest being in the deepest cells.

With such scanty data, we can only be indefinite about social relationships. It seems probable that the nest from Guaruva was made and the eight cells provisioned by the single female that was found in it. One of the nests opened February 21 contained only four cells and was occupied by a single fertilized female with well worn mandibles, much tattered wings, and rather slender ovaries, which may account for the fact that of the four cells, only one was or had been occupied (it contained a small larva). A group of old, earth-filled cells indicated that the nest was being reused. The other nest opened on the same day contained about eight

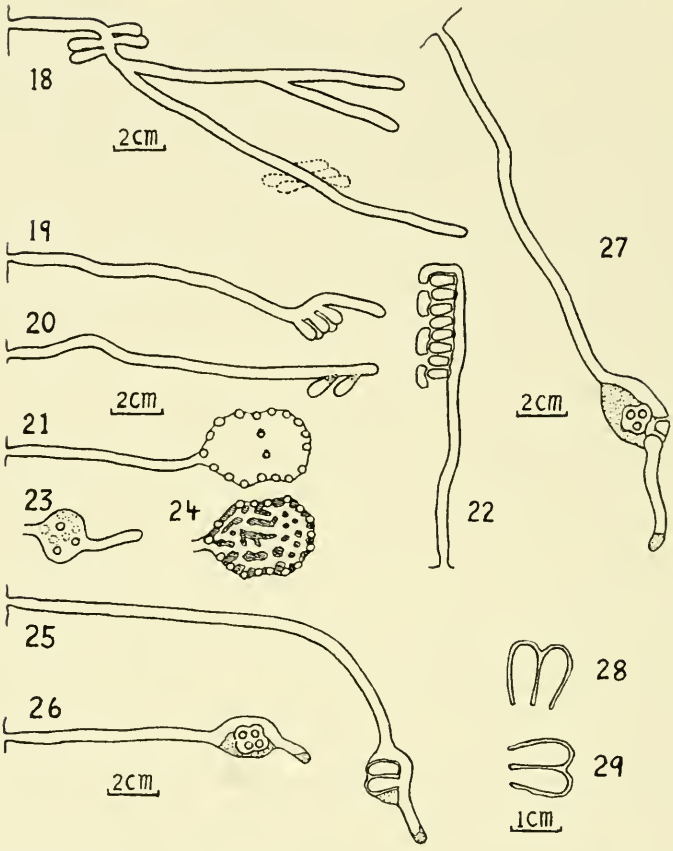

FIG. 18. Diagram of nest of *Augochlora morrae*. Cells indicated by dotted lines were old and earth filled (February 21, 1956).

FIGS. 19-21. Diagrams of nest of *Augochlorella michaelis* (Dec. 4, 1955; Jan. 13 and February 21, 1956, respectively). Fig. 19 and 20 are side views of nests with strongly slanting cells. Fig. 21 is side view of a nest with cells but slightly slanting. The marginal holes around the cell cluster (which has two open cells) lead to the passageways behind the cell cluster.

FIG. 22. Top view of nest shown in fig. 21, showing passageways behind cells.

FIG. 23. Front view of the cell cluster shown in fig. 19 (closed cells are shown dotted).

FIG. 24. Back view of cell cluster of nest shown in figs. 21 and 22. Shaded areas are earth supports between the passageways behind the cells.

FIG. 25. Diagram of nest of *Paroxystoglossa andromache* showing cell cluster in side view in contact with chamber wall and supported by loose dirt (Oct. 23, 1955).

FIGS. 26-27. Diagrams of nests of *Paroxystoglossa andromache* showing cell clusters in front view, in one case with pillars (Oct. 23 and 24, 1955).

FIG. 28. Top view of horizontal section of cell cluster of *Paroxystoglossa andromache* (Oct. 24, 1955).

FIG. 29. Side view, vertical section, of same.

cells, several parasitized by mutillids, others containing small larvae and pupae. There were three unfertilized, unworn young adult females with slender ovaries in the nest, probably recently emerged, but the bee or bees that made the nest seemingly had not survived. The nest from Rio de Janeiro similarly contained only young unfertilized females, in this instance four of them. In this case, however, the nest was dug on a warm day without a preliminary period of watching and it is possible that older bees were afield.

The nests are burrows about 5 mm. in diameter, narrowed at the entrance, and extending horizontally into a bank or slope slightly downward, or are vertical in flat ground. The burrows are 10 to 20 cm. deep and may be simple or branched. The cells are essentially horizontal, very like those of *Chloralictus*, but in denser clusters than usual in that group. Among the nests which we studied the cells were in groups of four to nineteen. The cells are lined with waxlike material, the lower sides flatter than the upper. The pollen is in the form of a flattened firm ball, with horizontal diameters 2.9 to 3.2 mm., the vertical diameter 2.1 mm.

Augochlorella michaelis (Vachal)

Only three nests of this species have been studied. One, in the Barigui roadside banks near Curitiba, Paraná, was found about November 4, 1955, and a bee was seen going in and out. It was excavated on December 4, at which time the entrance was closed. It contained a single fertilized female with well worn mandibles and wings, and in the six cells, young of various stages from egg to female pupa. Four of the cells eventually produced females, none males. Another nest was found in a bank at Araucaria, Paraná, January 13, 1956. It also contained an old fertilized female (mandibles much worn, wings tattered). Its two cells both contained female pupae. The small size of the nest combined with the worn condition of the female suggest that the nest may have been made by a senile bee that had worked elsewhere previously. The third was found in a bank near São José dos Pinhais, Paraná, on February 21, 1956. This last nest contained, in its cells, seven eggs, a half grown larva, four mature larvae, three prepupae, fifteen male pupae and six female pupae.

Unlike the first two nests mentioned, the last contained several bees. Three were captured as they returned to the nest with pollen loads on the scopa. These had slightly worn mandibles, indicating at least moderate age, but their ovaries were slender (longest oocyte .2 to .3 mm.) and they were unfertilized. Clearly they were worker-

like individuals. Three other females were in the nest when it was opened. One was unfertilized, unworn, with slender ovaries and was doubtless recently emerged. Two were fertilized and had very much worn mandibles, worn wings, and enlarged ovaries (longest oocyte 1.7 mm. in both cases). Clearly these two were egg layers. Their wing lengths were 5 and 5.1 mm.; those of the three workerlike bees were 4.6, 4.7, and 4.8 mm. The social relationships seem similar to those of *Pseudaugochlora nigromarginata*, in which there is also a suggestion of a size difference between the workerlike and the egg-laying females.

The three nests of this species that we studied were very different from one another, so that one is forced to doubt if they were really made by the same species of *Augochlorella*. Each consisted of a nearly horizontal, rather straight, unbranched burrow 7.5 to 10 cm. deep and 4 mm. in diameter, narrowed at the entrance. The burrow in the Bariguí nest ended in a sloping space on one side of which was a cluster of six completed closed cells and three rough, unlined cells (figs. 19, 23.) These cells were built of walls made by the bee, having a thickness of .7 to 1.0 mm. The subcircular cell cluster could be lifted out of its position intact, but there was no space around the cells except for the flat space over the cell entrances. The convexities of the closed ends of the cells were represented by concavities in the unworked earth in which the nest lay. From the space over the cells, a short burrow extended on into the bank. The axes of the cells were at an angle of about 45° to horizontal, as was the plane of the flat space providing access to them. The nest from Araucaria, having but two cells, lacked a space, the slanting cells merely extending downward from the burrow (fig. 20).

The nest from São José dos Pinhais was similar to the Bariguí nest in having a flat subcircular cluster or plate of cells, but this cluster was more nearly vertical, so that the cells themselves were more nearly horizontal. There were 38 cells, two of them empty, in the cluster. Around its margins a series of holes extended inward and connected with interconnecting passages between the backs of the cells and the soil, so that the cell cluster was supported by the spaces and pillars among these passages and by the soil between the holes leading to these passages (figs. 21, 22, 24). The passages had been excavated in the unworked soil behind the cells, leaving the convexities of the closed ends of the cells visible. The cell walls were .5 to 1.0 mm. thick throughout.

Cells, lined with waxlike material, are flatter on the lower surfaces than the upper, and are 9 to 9.8 mm. long, 4 to 5 mm. wide at the widest point, and 2.5 to 3 mm. wide at the neck. The pollen ball, which is a flattened sphere, about 3.3 mm. in the greatest diameter and about 2 mm. in the smallest (morphologically vertical) diameter, is placed on the flatter side of the cell near the closed end, as usual in halictids. The egg is 2.1 mm. long, arcuate, white, and placed on the upper surface of the pollen ball.

Paroxystoglossa andromache (Schrottky)

The biology of this species is probably similar to that of *P. jocasta* (Schrottky) (see Michener and Lange, 1958a). Our first record of it is of a burrow being dug on August 30, 1955 and a few nests were found in various stages of construction during September, October, and January, 1956. Cells being provisioned or containing eggs were found on October 14, 23, and 24, and cells with pupae were found on January 27. Unlike *P. jocasta*, nests are usually found in banks or steeply sloping ground. We found them in the Bariguí roadside banks (see Michener, Lange, Bigarella and Salamuni, 1958) and in a bank at Xaxim near Curitiba, in a bank near São José dos Pinhais, and in a bank near Campo Largo, all in the state of Paraná.

On a cold day (September 16, 1955) three males were found, one in a burrow 3 cm. deep in a bank, two in burrows of *Augochloropsis diversipennis* (Lepeletier).

Of twelve nests opened, only one contained two adult female bees. As in such cases in *P. jocasta*, one of the bees had enlarged ovaries, the other slender ovaries, but both had been fertilized.

The nests are similar to those of *P. jocasta* except that the burrow, which is 9 to 25 cm. deep, is horizontal or slants downward instead of being vertical. The cell cluster, like that of *jocasta*, consists of very thin-walled cells, usually very few in number (figs. 28, 29). The largest clusters we found contained only four cells. The cell cluster is placed in a chamber in which it may be supported by pillars as in *jocasta* but usually the lower part of the chamber, between the cluster and the wall of the chamber, is filled with friable soil which supports the cluster (figs. 25 to 27). Pillars may or may not be entirely absent in such cases.

The cells are horizontal and lined with waxlike material, and shaped as in *P. jocasta*. They are 11 to 12 mm. long, 5 to 5.25 mm. wide, the neck about 2.75 mm. wide; the pollen ball is slightly

flattened, about 4 mm. in horizontal diameter. The white arcuate egg is about 2 mm. long.

Habralictus canaliculatus Moure

Seasonal Cycle: This is a minute and inconspicuous, and apparently rather rare bee about which we can contribute but little. Three nests were found on October 23, 1955, in a small moss covered bank about 20 cm. high, completely shaded in the forest near the Bariguí roadside banks, Curitiba, Paraná. Later these nests could not be located in spite of weekly visits and were evidently closed but on January 8, 1956, loose dirt, indicating recent excavation, was noted at the same place and on January 15 one of the nests was dug. Two males and three unworn young females but no immature stages were found in it. It seems very probable that in spring (October) the nests were provisioned. Apparently they then became closed and another brood emerged in January. On February 29 a nest was found in one of the Bariguí roadside banks (see Michener, Lange, Bigarella and Salamuni, 1958). It contained four cells, one of them with a half-grown larva, two with eggs, and one being provisioned. On March 11 a nest in the same area, containing but one cell which was being provisioned, was found. On March 16 a nest was found containing two half-grown larvae, numerous mature larvae and prepupae, and twelve male and three female pupae (white). On March 18 another nest with three prepupae in it was found.

These data suggest a brood that matures in the fall and provisions cells in the spring. The summer brood from these cells, appearing in January and provisioning cells through February and early March, gives rise to the brood that matures in the fall. The two broods would be comparable to those of *Pseudagapostemon* (Michener and Lange, 1958).

Social organization: Of the very few nests examined, two were known to be occupied by but one female, and contained few cells, although they were still being enlarged and more cells would probably have been built. The large nest opened on March 16 contained 37 cells and a single old female with much worn mandibles. It seems very probable that this one bee did not make and provision so many cells. Probably several bees had lived together in this nest. The presence of some old dirt-filled cells in addition to the 37 occupied ones indicated that this nest had been occupied during the previous generation.

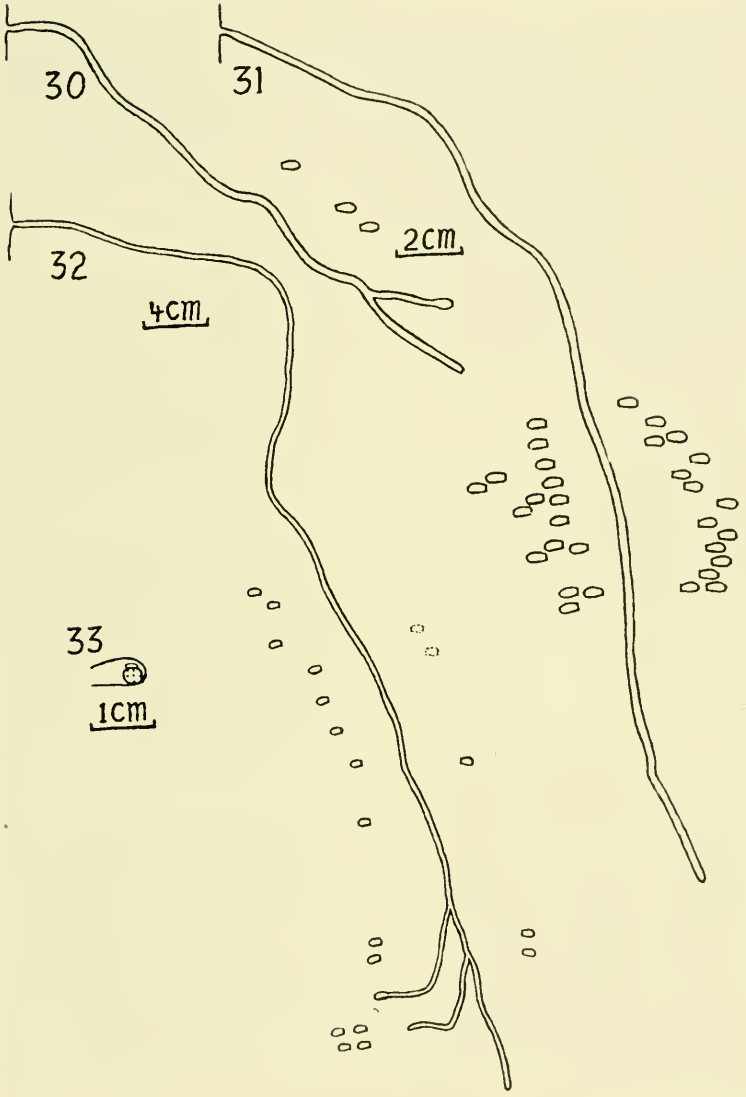

Fig. 30. Diagram of nest of *Habralictus canaliculatus* (Feb. 29, 1956).
Fig. 31. Diagram of nest of same (Mar. 16, 1956).
Fig. 32. Diagram of nest of *Caenaugochlora curticeps* (Oct. 17, 1955).
Fig. 33. Diagram of cell, with pollen mass and egg, of same.

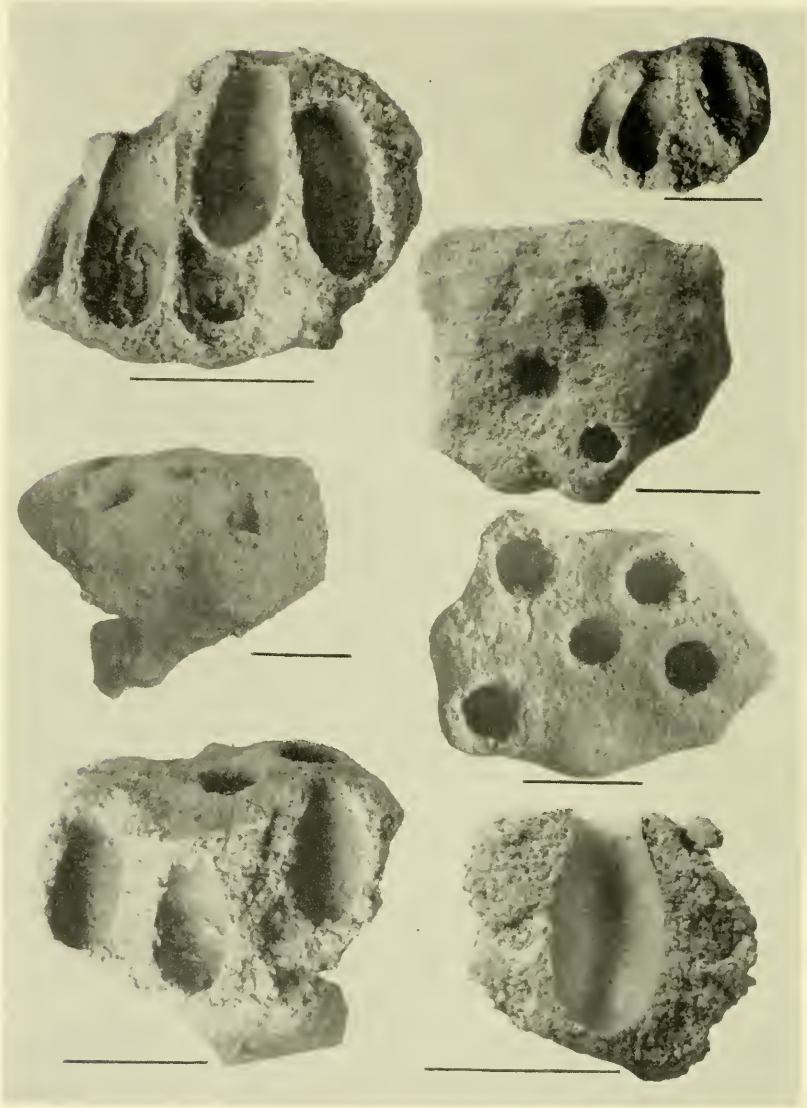

FIG. 34. Cell clusters of *Neocorynura polybioides*. Black lines represent 1 cm. *Top three* photographs show vertical sections and a top view of the cluster from a nest opened on Dec. 21. The central cell, at upper left, has been used three times. *Middle and lower left* show side view and a vertical section of a cluster that was unusual in being supported by a single large pillar (Dec. 21). *Middle right* is a top view of the same cluster. Two cells were closed, but their contents moldy. *Lower right* is a vertical section of a cell "cluster" (of one cell) in the nest of an unworn stylopized female (Dec. 21).

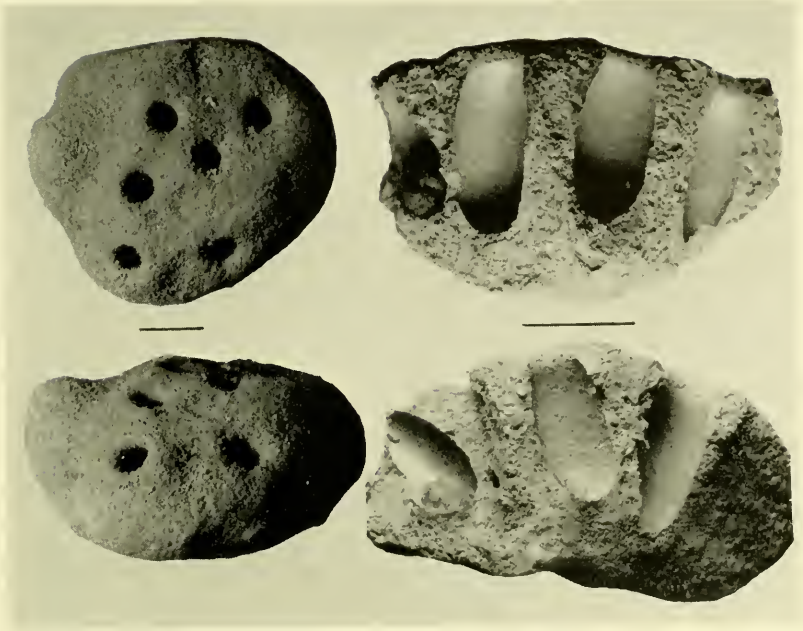

Fig. 35. Cell clusters of *Pseudaugochlora nigromarginata*. Black lines represent 1 cm. *At left*, top and side views of a cluster from a nest opened on Sept. 29. Faintly depressed areas are plugs of provisioned closed cells. *At right* are vertical sections through a cell cluster. The upper one shows a provisioned cell (left) and smooth but unwaxed cells (center) at least one of which had been used previously as shown by old fecal matter below the base of the present cell. The lower one shows the same provisioned cell (left), a shaped but not smoothed cell (center) and a smoothed but unwaxed cell (right).

Except for obviously young bees, every female dissected (six, including a few captured flying about banks in the Floresta da Tijuca, Rio de Janeiro, January 9, 1956, by Dr. Carlos Alberto Campos Seabra) had been fertilized and had enlarged ovaries with eggs. Thus there is no suggestion of a worker caste. When several females occupy one nest, their interrelationships may be similar to those of *Pseudagapostemon*.

Nests: Each nest consists of a slender, unbranched burrow extending into the bank and sloping downward. The burrow is 2.5 to 2.8 mm. in diameter, narrowed at the entrance to 1.5 mm. in diameter. These burrows reach a length of at least 32 cm. (large nest opened March 16); smaller and incomplete nests which might have been further deepened had burrows 12 and 18 cm. in length.

The cells are horizontal or but slightly slanting, 2 to 4 cm. from

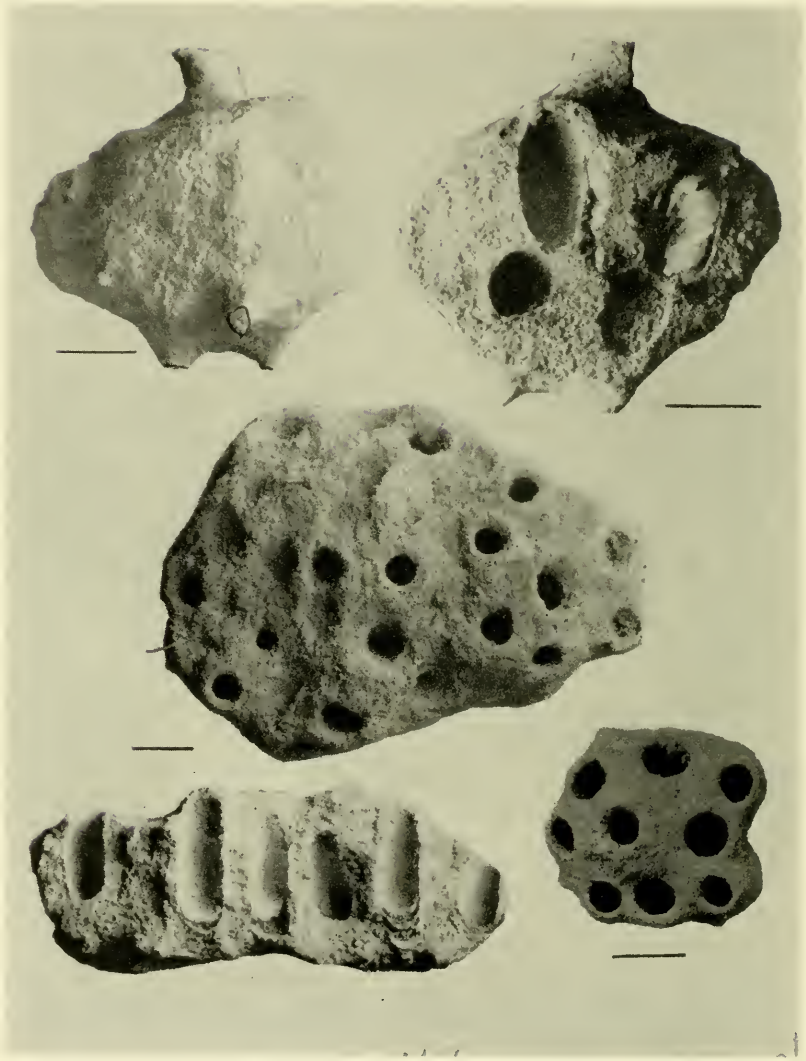

FIG. 36. Cell clusters of *Pseudaugochlora nigromarginata*. Black lines represent 1 cm. *Top*, side view and vertical section of cluster which had three supporting pillars below (broken surfaces outlined in black in side view) and an unusual pillar from top of cluster to roof of chamber. The section shows a horizontal cell (lower left) and an old earth filled slanting cell (lower right) (Nest opened Nov. 22). *Center*, top view of old cell cluster in which one cell (lower left) has been prepared for use. Rootlets which supported this cluster can be seen (Nov. 22). *Lower left*, vertical section of the same, showing fresh cell at left, and other cells, some of which, although abandoned, were closed at the surface. Reuse of several cells is evident. Fecal material is well shown in the third cell from the right. The second cell from the right shows particularly well how waxlike linings of various cells have been rasped away, apparently by mandibular action in enlarging the cell entrance. *Lower right*, top view of small cluster. All cells were open; entrances of some of them had been much enlarged.

the main burrow. In the smaller nests, being built by lone females, the youngest cell was that farthest from the nest entrance and the oldest cell was nearest the entrance. Each cell had presumably been constructed at the end of a different lateral burrow, but all laterals except that leading to the cell being provisioned were so well filled with soil as to be unrecognizable. In the large nest opened on March 16 the younger and older brood was not systematically arranged, and the cells were grouped in such a way as to suggest that several may have been constructed branching from the same lateral. However, since all the laterals were completely and indistinguishably earth filled, this is not certain.

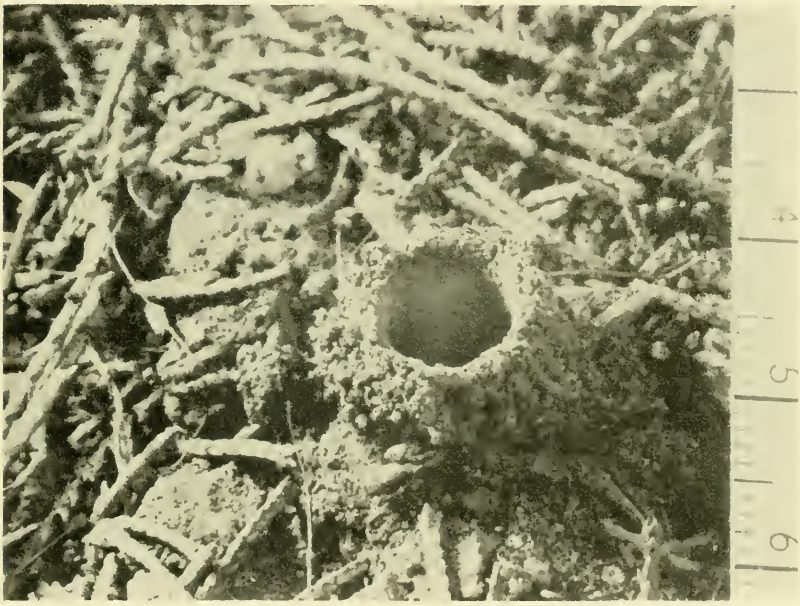

Fig. 37. Turret at nest entrance of *Megommation insigne*. Scale at right is in centimeters.

The cells measure 5 to 6 mm. in length, 2.8 to 3.3 mm. in maximum diameter, with the diameter of the neck about 1.8 mm. The cells are lined with waxlike material except for the necks. The lower surface or floor of a cell is flatter than the upper and the pollen ball lies on the floor near the distal end of the cell. Horizontal diameters of a pollen ball were 2.1 and 2.3 mm., the vertical diameter was 1.9 mm. The curved egg is placed on top of the pollen ball, in contact with it at both ends.

Caenaugochlora curticeps (Vachal)

Seasonal cycle: The few nests of this small species that were studied were scattered along the Bariguí roadside banks; their distribution there was indicated by Michener, Lange, Bigarella and Salamuni (1958).

The first nest found was on October 14, 1955. At this time both sexes were on the wing. The nest found on October 14 was opened three days later. It consisted of a burrow, with no cells. The females captured at this time were not or only slightly worn. The last spring male was seen on October 23. The next nest found was opened on October 29. It contained provisioned cells with eggs but no larvae. A nest opened on November 16 already had mature larvae, as well as small larvae and eggs. After the later part of November, no individuals of this species were seen until January 21, 1956 when both sexes were noted flying along the banks. On February 29, it was noted that while adults had not been seen for some time, a well worn female was found in a burrow. On March 11 a few females were again seen flying along the banks.

The number of observations of this small and uncommon species is small, but we may surmise that the seasonal cycle is similar to that of *Habralictus canaliculatus* (see above) and *Pseudagapostemon* (Michener and Lange, 1958). There seems to be a brood that appears in the fall (March); both sexes survive the winter and the females provision nests in spring (October, November). The progeny of this brood appear and provision nests in summer (January, February).

Social organization: Only three nests could be opened completely because of rarity of the bee and the difficulty of following the deep, slender burrows. Two of the three nests contained three females, one contained four. Observations of activities at nest entrances indicated that some nests contained at least five females. In these nests, during warm sunny weather, one or another of the females commonly plugged the entrance with her head.

As with *Pseudagapostemon* (possibly also *Habralictus canaliculatus*) activities seemed well synchronized. The bees taken from any one nest at one time had similarly developed ovaries, similarly worn mandibles, etc. Except for obviously young bees, all females found had been fertilized. There is, thus, no indication of a worker caste. Perhaps the interrelationships among females in a nest are similar to those that occur in *Pseudagapostemon*.

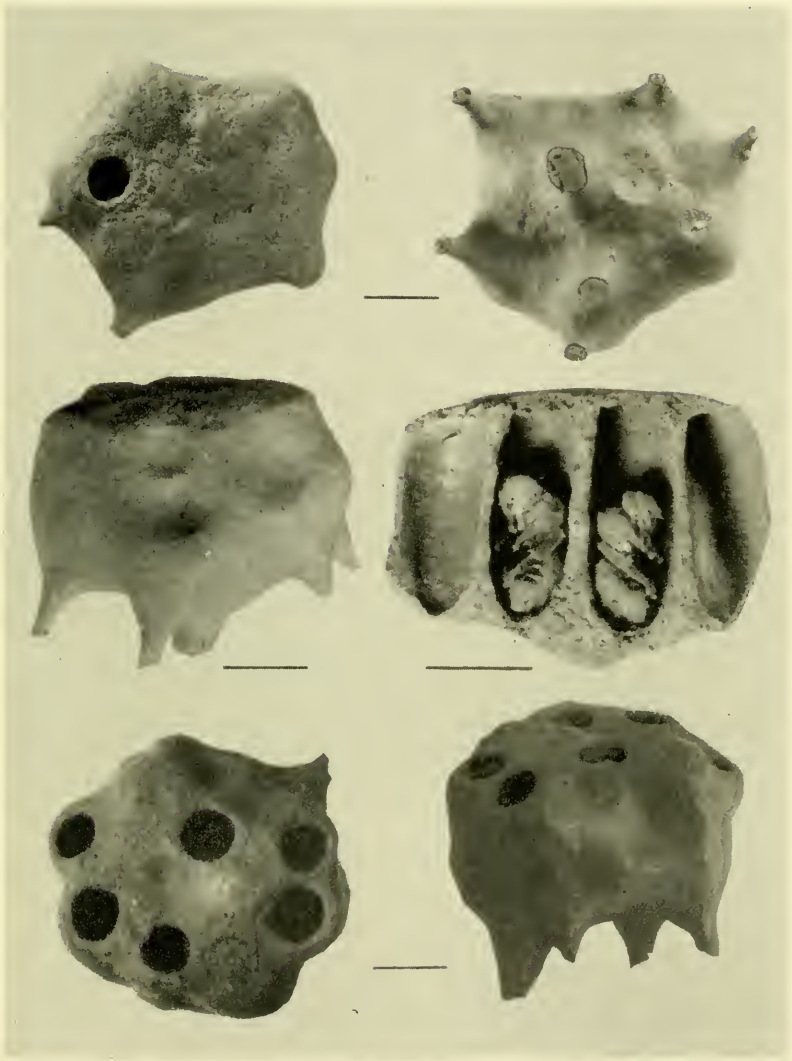

FIG. 38. Cell clusters of *Megommation insigne*. Black lines represent 1 cm. *Top left*, top view of cluster with one cell open, others closed and with immature stages (Nest opened Jan. 5). *Top right*, bottom view of same cluster. Broken ends of pillars are circled in black. *Middle left*, side view of same cluster. *Middle right*, vertical section of same cluster. *Bottom*, top and side views of cluster from nest opened on Feb. 16 (retouched to emphasize cell openings).

Nests: Each nest consists of a simple or branched burrow which extends into the bank, slanting slightly downward for 18 to 39 cm. and then turns more steeply downward. Total depth of the burrow ranges from 65 to 90 cm. In diameter the burrow ranges from 3 to 4 mm., narrowed to about 2.75 mm. at the entrance.

The cells are nearly horizontal, sloping slightly downward, and located one to four centimeters from the main burrow. As with *Habralictus canaliculatus,* they are often so arranged that each cell must have been constructed at the end of a separate lateral burrow, but sometimes they are in groups suggesting that several cells may have been connected to a single lateral. Also as in the

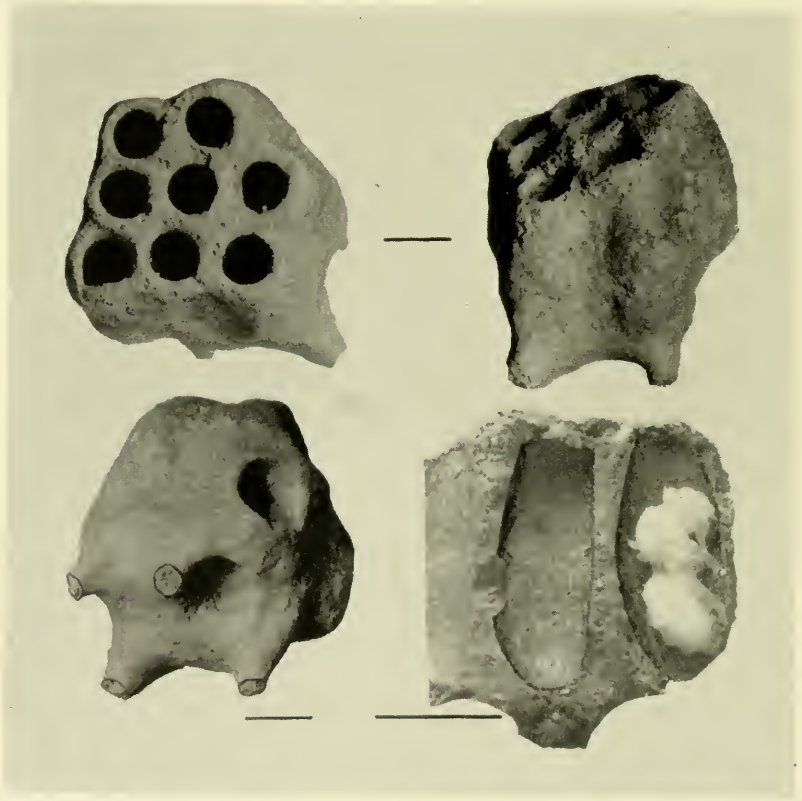

FIG. 39. Cell clusters of *Megommation insigne.* Black lines represent 1 cm. *Top,* top and side views of cluster from nest opened on May 4. *Lower left,* oblique bottom view of same. Black circles enclose broken surfaces of pillars. A curious canal, bridged in the center, was the outstanding feature of this cluster. *Lower right,* pupa in cell (Dec. 16). The reticulate pattern of pale lines in the waxed parts of the cells appears only after drying, and perhaps results from differential shrinkage (retouched to emphasize cell shape).

Habralictus, once a cell is provisioned and an egg laid in it, the lateral burrow is completely filled with dirt so that it is unrecognizable. In nests opened during the season of cell construction and provisioning, it was the lowermost one or two lateral burrows that were open, suggesting that the nests are deepened and new laterals constructed at the bottom as the season progresses.

The cells measure 8 to 9 mm. long, about 4.4 mm. in maximum diameter, about 2 mm. in diameter at the neck. They are lined with a waxlike substance except at the entrance. The pollen ball lies near the closed end of the cell, is nearly spherical, about 2.8 mm. in diameter. The curved white egg, about 1.5 mm. long, is placed on top of the pollen ball. The egg is but little narrower posteriorly than anteriorly.

The species of *Caenaugochlora* whose nests were described by Claude-Joseph (1926), *C. chloris* (Spinola), *opaciceps* (Friese) [= *scitulus* (Vachal)], and *rostraticeps* (Friese), construct nests with a cell cluster somewhat like that of *Augochlorella michaelis* or *Augochlora semiramis.* It seems probable that they belong in a genus distinct from that of *curticeps.*

CONCLUSIONS

Table I summarizes certain of the data presented above. It is noteworthy that among the few species studied, a good series of progressive steps in establishment of social behavior can be recognized. *Paroxystoglossa* nests are usually made by individual females, although occasionally two females nest together. The same may be true of *Neocorynura* except that nests inhabited by two bees are perhaps more common. In *Caenaugochlora* and probably *Habralictus,* as in *Pseudagapostemon,* several females inhabit the same nest but all are fertilized and all lay eggs. In *Augochlora semiramis* the same is true except that when we opened the nests only one female was in egg laying condition. The others probably have workerlike functions, even though fertilized, as they do in *Augochloropsis sparsilis.* In *Psendaugochlora, Megammation,* and *Augochlorella,* unfertilized workerlike individuals exist with an egg laying individual in each nest. More clearly distinguishable workers and queens are not found among the species discussed in this paper.

Another feature that seems to show progressive development is the clumping of the cells and establishment of air spaces surrounding them. As this is a feature which arises in various lines of halic-

TABLE 1. *Summary of some biological characters of certain Halictinae*

	Neocorynura	Pseud-augochlora	Megammation	Augochlora semiramis	Augochlorella morrae	Augochlorella michaelis	Paroxy-stoglossa	Habra-lictus	Caenaugochlora
cells	usually vertical, in cluster in chamber	usually vertical, in cluster in chamber	vertical, in cluster in chamber	horizontal, in groups with slight surrounding excavation	horizontal, in groups	horizontal or slanting in groups with partial surrounding excavation	horizontal, in cluster in chamber	horizontal, isolated in soil	horizontal, isolated in soil
no. of ♀♀ per nest	1–2	1–3	1–4	1–8	?	1–6	1 (rarely 2)	1–several?	3–5
workerlike individuals	unknown	unfertilized present	unfertilized present	fertilized present?	?	unfertilized present	unknown	unknown	unknown

tine evolution, it must have some important selective advantage. Perhaps it makes possible a degree of control of the environment of the cells and the immature stages which they contain. In *Habralictus* and *Caenaugochlora*, as in most other burrowing bees, the cells are scattered with no surrounding air spaces. In *Augochlora morrae* they are clustered, with no surrounding spaces. In *A. semiramis* they are clustered, with burrows often passing near them. In *Augochlorella* (larger nest), the cells are clustered with anastomosing burrows excavated behind them. In *Neocorynura* and *Pseudaugochlora*, a space surrounds the cell cluster, which is supported only by pillars of soil (or by rootlets). The same is true of *Megammation* but the cell cluster is made of thinner earth, a tendency which reaches its extreme in *Paroxystoglossa*, although in the species here discussed some of the air space is usually filled with loose dirt.

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SCIENCE BULLETIN

VOL. XXXIX] NOVEMBER 18, 1958 [NO. 12

Catalogue of the Types in the Snow Entomological Museum. Part II (Mallophaga)*

BY

K. C. EMERSON

ABSTRACT: Types of 68 species and subspecies of Mallophaga are listed, together with references, notes on host, present taxonomic status, and type numbers as recorded in the catalogue of the types in the Snow Entomological Museum.

INTRODUCTION

The Snow Entomological Museum of the University of Kansas contains more Mallophaga type material than is generally known. This is because the disposition of all type material has been omitted in a majority of the taxonomic papers. Usually the author has given the disposition of the holotype and allotype, and recorded the number of paratypes. The disposition of paratypes has in most instances, been made by the collector, or curator of the collection from which the series was obtained. The presence of paratypes in the Snow Entomological Museum has not been noted in most papers, as this material was obtained as gifts following publication. The number of species represented is significant; and probably is exceeded, in the United States, in only three or four collections.

Except for the Kellogg type material, all is of recent origin; hence it has presented no unusual problems in the compilation of this list. A few explanatory remarks concerning the Kellogg material are necessary to clarify the position taken with regard to this material. Much of the material utilized by Kellogg, in his first three taxonomic papers on Mallophaga, was obtained during his tenure as a member of the faculty of the University of Kansas, and before joining the faculty of Stanford University. After the publication of

* Contribution No. 1030 of the Department of Entomology, University of Kansas, Lawrence, Kansas.

these papers, some of the type material was returned to the University of Kansas. This information is found in the author's preface of "North American Mallophaga," 1896, Leland Stanford Jr. University, in which he states: "Types of the new species described will be placed in the collections of this University, in the collections of the California Academy of Sciences, and in those of the University of Kansas." Kellogg did not designate a holotype, allotype or type for each species described, but considered all of the material examined as cotypes. In some instances, the series examined by Kellogg contained material which now represents more than one species. In these cases, M. A. Carriker, Jr., the author, and others examining the Kellogg material at Stanford University, have selected as lectotype the specimen from which illustrations were prepared. This was not difficult as the information was noted on the label. All other specimens, which are conspecific with the lectotype, and with the same collection data, are considered by the author to be syntypes. Material which is not conspecific with the lectotype, and that in which the collection data does not agree with that noted in the original description, has not been accepted as syntypes. Mr. M. A. Carriker, Jr., has prepared a paper in which lectotypes are designated for several species. The action taken by Carriker has been recognized during the preparation of this list. All type material is listed alphabetically according to the name given in the original description.

ACKNOWLEDGMENTS

I am greatly indebted to the late Dr. G. F. Ferris for the loan of many types in the Kellogg Collection at Stanford University; to Mr. M. A. Carriker, Jr., for providing me with the manuscript of his paper on the Kellogg Collection; and to Dr. C. D. Michener for assistance and suggestions given during the preparation of this report.

MALLOPHAGA

Actornithophilus mexicanus Emerson, 1953, J. Kansas Ent. Soc., vol. 26, p. 134. Type host: *Himantopus mexicanus* = *Himantopus himantopus mexicanus* (Müller). ♀ paratype, no. 4677, from type host collected May 18, 1933 by A. R. Phillip at Tucson, Arizona. Present status: *Actornithophilus himantopi mexicanus* Emerson, 1953.

Anatoecus autumnalis Carriker, 1956, Florida Ent., vol. 39, p. 126. Type host: *Dendrocygna autumnalis autumnalis* (Linnaeus). ♂ paratype and 2 ♀ paratypes, no. 5643, from type host collected

September 19, 1946 by O. Shaw at Tamuin, San Luis Potosí, Mexico. Present status: *Anatoecus autumnalis* Carriker, 1956.

Anatoecus clangulus Emerson, 1953, J. Kansas Ent. Soc., vol. 26, p. 136. Type host: *Clangula hymenalis* (Linnaeus). ♂ paratype and ♀ paratype, no. 4675, from type host collected January 2, 1950 at Tucson, Arizona. Present status: *Anatoecus clangulus* Emerson, 1953.

Bovicola americanum Jellison, 1935, J. Parasit., vol. 21, p. 410. Type host: *Cervus canadensis* (Erxleben). Two ♀ paratypes, no. 5644, from type host collected February, 1935 by C. B. Philip in Yellowstone Park. Present status: *Bovicola americanus* Jellison, 1935.

Brüelia laticeps prasinus Carriker, 1954, Florida Ent., vol. 37, p. 199. Type host: *Aulocorhynchus prasinus prasinus* (Gould). Two ♀ paratypes, no. 5674, from type host collected February 7, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Brüelia laticeps prasinus* Carriker, 1954.

Brüelia marginella xilitla Carriker, 1954, Florida Ent., vol. 37, p. 200. Type host: *Momotus momota caeruleiceps* (Gould). ♂ paratype and ♀ paratype, no. 5675, from type host collected February 12, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Brüelia marginella xilitla* Carriker, 1954.

Brüelia melanococca abbasi Carriker, 1956, Florida Ent., vol. 39, p. 119. Type host: *Thraupis abbas* (Lichtenstein). Two ♀ paratypes, no. 5687, from type host collected January 27, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Brüelia melanococca abbasi* Carriker, 1956.

Brüelia saltatora Carriker, 1956, Florida Ent., vol. 39, p. 119. Type host: *Saltator coerulescens vigorsii* G. R. Gray. ♂ paratype, no. 5688, from type host collected January 22, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Brüelia saltatora* Carriker, 1956.

Carduiceps eroliae Carriker, 1956, Florida Ent., vol. 39, p. 123. Type host: *Erolia fuscicollis* (Vieillot). ♀ paratype, no. 5689, from type host collected May 21, 1947 by D. S. Farner at Lawrence, Kansas. Present status: *Carduiceps zonarius eroliae* Carriker, 1956.

Carduiceps lapponicus Emerson, 1953. Proc. Ent. Soc. Wash., vol. 55, p. 209. Type host: *Limosa lapponica lapponica* (Linnaeus). ♂ paratype and ♀ paratype, no. 5422, from a museum skin of

type host collected September, 1899 at Mainz, Germany. Present status: *Carduiceps cingulatus lapponicus* Emerson, 1953.

Carduiceps pusillus Carriker, 1956, Florida Ent., vol. 39, p. 125. Type host: *Ereunetes pusillus* (Linnaeus). 2 ♀ paratypes, no. 5690, from type host collected May 15, 1947 by George H. Lowery at Lawrence, Kansas. Present status: *Carduiceps zonarius pusillus* Carriker, 1956.

Colinicola mearnsi Emerson, 1948, J. Kansas Ent. Soc., vol. 21, p. 137. Type host: *Cyrtonyx montezumae mearnsi* Nelson. ♀ paratype, no. 4069, from type host collected November 25, 1938 by A. R. Phillip at Nogales, Arizona. Present status: *Colinicola mearnsi* Emerson, 1948.

Colpocephalum osborni Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 521. Type host: *Elanus glaucus* = *Elanus leucurus majusculus* Bangs and Penard. ♂ syntype and ♀ syntype, no. 1336, from type host collected at Palo Alto, California. Present status: *Colpocephalum osborni* Kellogg, 1896.

Craspedorhynchus brevicapitis Carriker, 1956, Florida Ent., vol. 39, p. 26. Type host: *Buteo magnirostris griseicauda* Ridgway. ♀ paratype, no. 5691, from type host collected February 12, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Craspedorhynchus brevicapitis* Carriker, 1956.

Craspedorhynchus genitalis Carriker, 1956, Florida Ent., vol. 39, p. 29. Type host: *Geranospiza nigra nigra* (Du Bus). ♂ paratype and two ♀ paratypes, no. 5692, from type host collected August 1, 1947 by Robert J. Newman at Heda Capulin, San Luis Potosí, Mexico. Present status: *Craspedorhynchus genitalis* Carriker, 1956.

Craspedorhynchus tubulus Carriker, 1956, Florida Ent., vol. 39, p. 26. Type host: *Busarellus nigricollis nigricollis* (Latham). ♂ paratype, no. 5693, from type host collected September 19, 1946, by C. Shaw at Tamuin, San Luis Potosí, Mexico. Present status: *Craspedorhynchus tubulus* Carriker, 1956.

Degeeriella carruthi Emerson, 1953, J. Kansas Ent. Soc., vol. 26, p. 132. Type host: *Falco sparverius sparverius* Linnaeus. ♂ paratype, no. 5663, from type host collected April 6, 1936 at Flagstaff, Arizona. Present status: *Degeeriella rufa carruthi* Emerson, 1953.

Docophorus atricolor Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 93. Type host: *Synthliborhampus antiquus* and *Brachyrhampus marmoratus* (both in error) = *Gavia arctica pacifica* (Lawrence); see Emerson, 1955, Ann. Mag. Nat. Hist., series 12, vol. 8,

p. 719. Two ♀ syntypes, no. 1321, with collection data "*Synthliborhampus antiquus*, Monterey Bay, California". Present status: *Craspedornirmus colymbinus* (Denny), 1842.

Docophorus californiensis Kellogg, 1896. Proc. Calif. Acad. Sci., vol. 6, p. 483. Type host: *Melanerpes formicivorus bairdi* Ridgway. Two male syntypes, no. 1324, from the type host collected at Palo Alto, California. Present status: *Penenirmus californiensis* (Kellogg), 1896.

Docophorus domesticus Kellogg, 1896. Proc. Calif. Acad. Sci., vol. 6, p. 475. Type host: *Progne subis subis* (Linnaeus). One male syntype, no. 1327, from type host collected at Lawrence, Kansas. Present status: *Philopterus domesticus* (Kellogg), 1896.

Docophorus exicsus major Kellogg, 1896. Proc. Cal. Acad. Sci., vol. 6, p. 490. Type host: *Petrochelidon lunifrons* = *Petrochelidon albifrons albifrons* Rafinesque (and *Tachycineta bicolor*, error; see Carriker, 1957, Microentomology, 22; p. 97). One ♀ syntype, no. 1328, from type host collected at Palo Alto, California. Present status: *Philopterus major* (Kellogg), 1896.

Docophorus insolitus Kellogg, 1896. Proc. Cal. Acad. Sci., vol. 6, p. 94. Type host: *Ptychoramphus aleuticus* (Pallas). One ♂ syntype, no. 1320, from type host collected in the Bay of Monterey, California. Present status: *Saemundssonia insolita* (Kellogg), 1896.

Docophorus montereyi Kellogg, 1896. Proc. Cal. Acad. Sci., vol. 6, p. 87. Type host: *Synthliborhampus antiquus* (Gmelin), *Brachyramphus marmoratus marmoratus* (Gmelin) (error), and *Ptychoramphus aleuticus* (Pallas) (error); from Carriker *in litt*. Two ♀ syntypes, no. 5694, from type host collected in Monterey Bay, California. Present status: *Saemundssonia montereyi* (Kellogg), 1896.

Docophorus occidentalis Kellogg, 1896, Proc. Cal. Acad. Sci., vol. 6, p. 89. Type host: *Fulmarus glacialis* vars *glupischa* and *rodgersii* = *Fulmarus glacialis rodgersii* Cassin. Three ♀ syntypes, no. 1323, from type host collected in the Bay of Monterey, California. Present status: *Saemundssonia occidentalis* (Kellogg), 1896.

Docophorus procax Kellogg and Chapman, 1899, Occ. Pap. Cal. Acad. Sci., vol. 6, p. 54. Type host: *Cepphus columba columba* Pallas. ♂ syntype and ♀ syntype, no. 5695, from type host collected in the Bay of Monterey, California. Present status: *Saemundssonia procax* (Kellogg and Chapman), 1899.

Eurymetopus pacificus Kellogg, 1914, Sci. Bull. Brooklyn Inst., vol. 2, p. 87. *Nomen novum* for "*Eurymetopus taurus*," *sensu* Kellogg, 1896 (*nec* Nitzsch, 1866). Type host: *Diomedea albatrus* Pallas. 2 ♂ syntypes, no. 5696, from type host collected in Monterey Bay, California. This slide is labeled "*Nirmus giganticola*," which is an obvious error. Present status: *Docophoroides pacificus* (Kellogg), 1914.

Fulicoffula heliornis Carriker, 1953, Florida Ent., vol. 36, p. 155. Type host: *Helornis fulica* (Boddaert). ♀ paratype, no. 5697, from type host collected July 16, 1947 by Robert J. Newman on Rio Huichihuayan near Xilitla, San Luis Potosí, Mexico. Present status: *Fulicoffula heliornis* Carriker, 1953.

Giebelia mirabilis Kellogg, 1896, Proc. Cal. Acad. Sci., vol. 6, p. 138. Type host: *Puffinus opisthomelas* (Coues). Three ♀ syntypes, no. 5698, from type host collected in Monterey Bay, California. Present status: *Trabeculus mirabilis* (Kellogg), 1896.

Goniocotes creber Kellogg, 1896. Proc. Cal. Acad. Sci., vol. 6, p. 510. Type host: *Phasianus nychthemerus* = *Gennaeus nychthemerus* (Linnaeus). Two ♀ syntypes, no. 1335, from type host collected in a bird store in San Francisco, California. Present status: *Goniocotes albidus* Giebel, 1874.

Goniodes merriamanus Packard, 1873, report U. S. Geological Survey 1872, p. 731. Type host: *Tetrao richardsoni* = *Dendragapus obscurus richardsonii* (Douglas). ♀ neoparatype, no. 4070, from type host collected August 9, 1923 in Missoula County, Montana. Neotypes designated by Emerson, 1948, J. Kansas Ent. Soc., vol. 21, p. 93. Present status: *Goniodes merriamanus* Packard, 1873.

Gruimenopon canadensum Edwards, 1949, Psyche, vol. 56, p. 116. Type host: *Grus canadensis canadensis* (Linnaeus). ♂ paratype and ♀ paratype, no. 5361, from type host collected December 11, 1912 by F. B. Armstrong in Refugio County, Texas. Present status: *Gruimenopon canadense* Edwards, 1949.

Heptapsogaster inexpectatus potosii Carriker, 1954, Florida Ent., vol. 37, p. 205. Type host: *Crypturellus cinnamomeus mexicanus* (Salvadori). ♀ paratype, no. 5699, from type host collected April 21, 1947 by Robert J. Newman at Rio Axtla, San Luis Potosí, Mexico. Present status: *Heptapsogaster inexpectatus potosii* Carriker, 1954.

Lagopoecus colchicus Emerson, 1949, J. Kansas Ent. Soc., vol. 22, p. 78. Type host: *Phasianus colchicus torquatus* Gmelin. ♀

paratype, no. 4071, from type host collected March 9, 1945 by P. E. Telford at Logan, Utah. Present status: *Lagopoecus colchicus* Emerson, 1949.

Lagopoecus obscurus Emerson, 1948, J. Kansas Ent. Soc., vol. 21, p. 137. Type host: *Dendragapus obscurus richardsonii* (Douglas). ♀ paratype, no. 4054, from type host collected July 19, 1930 in the Harlan District, Ravalli County, Montana; and ♂ paratype, no. 4054, from type host collected May 9, 1920 in Ravalli County, Montana. Present status: *Lagopoecus obscurus* Emerson, 1948.

Lagopoecus umbellus Emerson, 1950, J. Kansas Ent. Soc., vol. 23, p. 101. Type host: *Bonasa umbellus* (probably *phaia* Aldrich and Friedmann). ♂ paratype and ♀ paratype, no. 4111, from type host collected March 30, 1941 by S. D. Beck in the Moscow Mountains, Latah County, Idaho. Present status: *Lagopoecus umbellus* Emerson, 1950.

Lipeurus deignani Emerson and Elbel, 1957. Proc. Ent. Soc. Wash., 59, p. 237, figs. 3 and 19. Type host: *Lophura diardi* (Bonaparte). One ♀ paratype, no. 5719, collected February 3, 1954, at Ban Sang Kho, Khok Phu, Sakon Nakhon, Thailand, by Robert E. Elbel. Present status: *Lipeurus deignani* Emerson and Elbel, 1957.

Lipeurus diversus Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 123. Type host: *Puffinus opisthomelas* (error) = *Puffinus griseus* (Gmelin); see Hopkins and Clay, 1952, A check list of the genera and species of Mallophaga, British Museum. ♀ syntype, no. 1332, with collection data "*Puffinus opisthomelas*, Monterey Bay, California". Present status: *Halipeurus diversus* (Kellogg), 1896.

Lipeurus gracilicornis var *major* Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 30. *Epifregata fregatiphagus* Eichler, 1943, Zool. Anz., vol. 141, p. 59, *Nomen novum* for *Lipeurus gracilicornis* var *major* Kellogg, 1899 (*nec. L. major* Piaget, 1880). Type host: *Fregata aquila* = *Fregata magnificens rothschildi* Mathews. ♂ syntype and ♀ syntype, no. 5700, from type host collected in Panamá. Present status: *Pectinopygus fregatiphagus* (Eichler), 1943.

Lipeurus limitatus Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 124. Type host: *Puffinus griseus* (Gmelin). ♀ syntype, no. 5358, from type host collected in the Bay of Monterey, California. Present status: *Halipeurus diversus* (Kellogg), 1896.

Lipeurus macrocephalus Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 504. Type host: *Chordeiles virginianus henryi* = *Chordeiles minor henryi* Cassin. Two ♀ syntypes, no. 1334, from type host collected at Palo Alto, California. Present status: *Mulcticola macrocephalus* (Kellogg), 1896.

Lipeurus protervus Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 31. Type host: *Lagopus lagopus* = *Lagopus lagopus alexandrae* Grinnell. Two ♀ syntypes, no. 5701, from type host collected on Kodiak Island, Alaska. Present status: *Lagopoecus affinis* (Children), 1836.

Menopon hopkinsi Emerson, 1954, Ann. Mag. Nat. Hist., series 12, vol. 7, p. 229. Type host: *Polyplectron malacensis* (Scopoli). ♀ paratype, no. 5665, collected from museum skin of type host collected in Malaya. Present status: *Menopon hopkinsi* Emerson, 1954.

Menopon infrequens Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 161. Type host: *Larus glaucescens* Naumann. ♂ syntype and ♀ syntype, no. 5702 from type host collected in Monterey Bay, California. Kellogg, in his description, states: "a single female taken from Glaucous-winged Gull, *Larus glaucescens* (Bay of Monterey, California)". It appears that Kellogg made an error in recording the number of specimens examined, as there are also types in the U. S. National Museum and Stanford University. The slide labels clearly indicate that all are a part of the same series. Present status: *Austromenopon infrequens* (Kellogg), 1896.

Menopon incertum Kellogg, 1896. Proc. Calif. Acad. Sci., vol. 6, p. 533. Type host: *Spinus tristis* = *Carduelis tristis salicamans* (Grinnell) and *Turdus ustulatus* = *Hylocichla ustulata ustulata* (Nuttall). One ♀ syntype, no. 1319, from *Turdus ustulatus* collected at Palo Alto, California. The type host of this species cannot be determined until the remainder of the type series can be examined. Present status: *Myrsidea incerta* (Kellogg), 1896.

Menopon numerosum Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 159. Type host: *Fulmarus glacialis* vars *glupischa* and *rodgersii* = *Fulmarus glacialis rodgersii* Cassin. ♂ syntype and two ♀ syntypes, no. 1317, from type host collected in Monterey Bay, California. This slide is labeled "*Lipeurus varius*" which is obviously in error. The handwriting is the same as that on other Kellogg slides. Present status: *Procellariphaga brevifimbriata* (Piaget), 1880.

Menopon praecursor Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 46. Type host: *Melanerpes uropygialis* = *Melanerpes hypopolius uropygialis* (Baird). ♂ syntype and ♀ syntype, no. 1331, from type host collected in Baja California. Present status: *Menacanthus praecursor* (Kellogg), 1899.

Menopon titan var *linearis* Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 165. Type host: *Pelecanus californicus* = *Pelecanus occidentalis californicus* Ridgway. ♀ syntype, no. 1318, from type host collected in Monterey Bay, California. Present status: *Piagetiella bursaepelecani* (Perry), 1876.

Menopon tridens var *pacificum* Kellogg, 1896, Proc. Calif. Acad. Sci., vol. 6, p. 166. Type host: *Urinator pacificus* (error) and *Fulica americana americana* Gmelin; see Emerson, 1949, Psyche, vol. 56, p. 91. One ♂ syntype and 1 ♀ syntype, no. 1316, from type host collected in Monterey Bay, California. The ♂ is labeled "*Lipeurus ferox*" which is obviously in error; the ♀ is labeled "*Urinator pacificus*, Bay of Monterey, Calif." The handwriting is the same as that on other Kellogg slides. Present status: *Pseudomenopon pacificum* (Kellogg), 1896.

Meropoecus smithi Emerson and Elbel, 1956, Ent. News, vol. 67, p. 118. Type host: *Merops leschenaulti leschenaulti* Vieillot. ♂ paratype and ♀ paratype, no. 5703, from type host collected December 22, 1952 by Robert E. Elbel at Ban Khlua Klang, Prachuap Kiri Khan, Thailand. Present status: *Meropoecus smithi* Emerson and Elbel, 1956.

Mulcticola deignani Emerson and Elbel, 1957, Canad. Ent., vol. 89, p. 420. Type host: *Caprimulgus macrurus bimaculatus* Peale. One ♂ and 4 ♀ paratypes, no. 5667, from type host collected July 20, 1953 by Robert E. Elbel on Nip Mountain, Lopburi, Thailand. Present status: *Mulcticola deignani* Emerson and Elbel, 1957.

Nirmus actophilus Kellogg and Chapman, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 78. Type host: *Calidris arenaria* = *Crocethia alba* (Pallas). ♂ syntype and ♀ syntype, no. 5704, from type host collected in the Bay of Monterey, California. Present status: *Lunaceps holophaeus actophilus* (Kellogg and Chapman), 1899.

Nirmus complexivus Kellogg and Chapman, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 75. Type host: *Tringa minutilla* (error) and *Calidris arenaria* = *Crocethia alba* (Pallas); from Carriker *in litt.* Two ♂ syntypes, no. 1329, from type host collected in

the Bay of Monterey, California. Present status: *Carduiceps zonarius complexivus* (Kellogg and Chapman), 1899.

Nirmus fusco-marginatus var *americanus* Kellogg and Chapman, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 69. Type host: *Colymbus nigricollis californicus* (Heermann). ♂ syntype and ♀ syntype, no. 1330, from type host collected in the Bay of Monterey, California. Present status: *Aquanirmus americanus* (Kellogg and Chapman), 1899.

Nirmus pacificus Kellogg and Chapman, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 70. Type host: *Lunda cirrhata* (Pallas) (error) and *Cepphus columba columba* Pallas; from Carriker *in litt.* ♂ syntype and ♀ syntype, no. 5359, from type host collected in the Bay of Monterey, California. Present status: *Quadraceps pacificus* (Kellogg and Chapman), 1899.

Nirmus peninsularis Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 21. Type host: *Phainopepla nitens* = *Phainopepla nitens lepida* van Tyne. Two ♀ syntypes, no. 5360, from type host collected in Baja California. Present status: *Brüelia peninsularis* (Kellogg), 1899.

Oxylipeurus abdominalis Carriker, 1956, Florida Ent., vol. 39, p. 129. Type host: *Dendrortyx barbatus* Gould. ♂ paratype and ♀ paratype, no. 5705, from type host collected June 12, 1947 by Robert J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Oxylipeurus abdominalis* Carriker, 1956.

Oxylipeurus annamensis Emerson and Elbel, 1957. Proc. Ent. Soc. Wash., 59, p. 238, figs. 2 and 13. Type host: *Lophura diardi* (Bonaparte). One female paratype, no. 5720, collected November 25, 1953 by Robert E. Elbel on Khao Sawan Mountain, Sieo, Loei, Thailand. Present status: *Oxylipeurus annamensis* Emerson and Elbel, 1957.

Pectinopygus tordoffi Elbel and Emerson, 1956, Ent. News, vol. 67, p. 173. Type host: *Pelecanus erythorhynchos* Gmelin. 2 ♂ paratypes and ♀ paratype, no. 5706, from type host collected October, 1954 by Harrison Tordoff at Lawrence, Kansas; and ♂ paratype from type host collected October, 1873 by F. H. Snow at Lawrence, Kansas. Present status: *Pectinopygus tordoffi* Elbel and Emerson, 1956.

Penenirmus auritus aurifrons Carriker, 1956, Florida Ent., vol. 39, p. 37. Type host: *Melanerpes aurifrons grateloupensis* (Lesson). Three ♂ paratypes and ♀ paratype, no. 5707, from type host collected February 25, 1947 by George H. Lowrey at San Luis Potosí.

Mexico. Present status: *Penenirmus auritus aurifrons* Carriker, 1956.

Penenirmus varius Emerson, 1953, J. Kansas Ent. Soc., vol. 26, p. 134. Type host: *Sphyrapicus varius varius* (Linnaeus). ♂ paratype and ♀ paratype, no. 4678, from *Sphyrapicus varius nuchalis* Baird collected April 2, 1936 in Arizona. Present status: *Penenirmus auritus varius* Emerson, 1953.

Philopterus phillipi Emerson, 1953, J. Kansas Ent. Soc., vol. 26, p. 132. Type host: *Cyanocephalus cyanocephalus* (Wied.). ♂ paratype, no. 4676, from type host collected April 26, 1936 at Flagstaff, Arizona. Present status: *Philopterus phillipi* Emerson, 1953.

Philopterus tropicalis Carriker, 1956, Florida Ent., vol. 39, p. 20. Type host: *Stelgidopteryx ruficollis serripennis* (Audubon). ♂ paratype, no. 5708, from type host collected January 4, 1947 by Robert J. Newman at San Luis Potosí, Mexico. Present status: *Philopterus tropicalis* Carriker, 1956.

Physconelloides passerinae Emerson, 1957, J. Kansas Ent. Soc., vol. 30, p. 37. Type host: *Columbigallina passerina passerina* (Linnaeus). ♂ paratype and ♀ paratype, no. 5666, from *Columbigallina passerina insularis* Ridgway collected August 16, 1930 by H. S. Peters at Guantanamo, Cuba. Present status: *Physconelloides passerinae* Emerson, 1957.

Physconelloides spenceri Emerson and Ward, 1958. J. Kansas Ent. Soc., 31: p. 239, figs. 1 and 4. Type host: *Columba fasciata fasciata* Say. One male and one female paratypes from type host collected October 6, 1952 by G. J. Spencer at Vancouver, British Columbia. Present status: *Physconelloides spenceri* Emerson and Ward, 1958.

Picicola praeposterus americana Carriker, 1956, Florida Ent., vol. 39, p. 71. Type host: *Melanerpes carolinus zebra* (Boddaert). Two ♀ and one nymph paratypes, no. 5709, from type host collected October 27, 1946 by George H. Lowrey at Lawrence, Kansas. Present status: *Picicola americana* Carriker, 1956.

Picicola rubina Carriker, 1956, Florida Ent., vol. 39, p. 73. Type host: *Pyrocephalus rubinus mexicanus* Sclater. ♀ paratype, no. 5710, from type host collected January 25, 1947 by R. J. Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Picicola rubina* Carriker, 1956.

Rallicola ortygometrae subporzanae Emerson, 1957, Proc. Ent. Soc. Wash., vol. 59, p. 186. Type host: *Porzana carolina* (Linnaeus). ♂ holotype and ♀ allotype, no. 5668, from type host collected

May, 1909 in Douglas County, Kansas. Present status: *Rallicola ortygometrae subporzanae* Emerson, 1957.

Saemundssonia haemastica Carriker, 1956, Florida Ent., vol. 39, p. 31. Type host: *Limosa haemastica* (Linnaeus). ♀ paratype, no. 5711, from type host collected May 15, 1947 by George H. Lowrey at Lawrence, Kansas. Present status: *Saemundssonia haemastica* Carriker, 1956.

Saemundssonia humeralis americana Carriker, 1956, Florida Ent., vol. 39, p. 31. Type host: *Numenius americanus americanus* Bechstein. ♀ paratype, no. 5712, from type host collected May 25, 1940 by Rollin Baker in Colorado County, Texas. Present status: *Saemundssonia humeralis americana* Carriker, 1956.

Strigiphilus ketupae Emerson and Elbel, 1957. Proc. Biol. Soc. Wash., vol. 70, p. 196, figs. 2 and 7. Type host: *Ketupa zeylonensis leschenault* (Temminck). One male and one female paratypes, no. 5721, from type host collected December 26, 1952 by Robert E. Elbel and H. G. Deignan at Huai Yang, Prachuap, Khiri Khan, Thailand. Present status: *Strigiphilus ketupae* Emerson and Elbel, 1957.

Strigiphilus macrogenitalis Emerson and Elbel, 1957. Proc. Biol. Soc. Wash., vol. 70, p. 197, figs. 4 and 9. Type host: *Glaucidium cuculoides brügeli* (Parrot). One male and one female paratypes, no. 5722, from type host collected January 5, 1952 by Robert E. Elbel at Ban Lat, Ban Kaeng, Khukhieo, Chaiyaphum, Thailand. Present status: *Strigiphilus macrogenitalis* Emerson and Elbel, 1957.

Strigiphilus otus Emerson, 1955, Proc. Ent. Soc. Wash., vol. 57, p. 241. Type host: *Otus asio gilmani* Swarth. ♀ paratype, no. 5664, from type host collected April 24, 1937 by A. R. Phillip at Tucson, Arizona. Present status: *Strigiphilus otus* Emerson, 1955.

Strigiphilus viridicus Carriker, 1954, Florida Ent., vol. 37, p. 195. Type host: *Ciccaba virgata centralis* Griscom. Two ♀ paratypes, no. 5613, from type host collected March 12, 1947 by Marcella Newman at Xilitla, San Luis Potosí, Mexico. Present status: *Strigiphilus viridicus* Carriker, 1954.

Sturnidoecus caligineus mexicanus Carriker, 1956, Florida Ent., vol. 39, p. 39. Type host: *Turdus infuscatus* (Lafresnaye). Two ♀ and one nymph paratypes no. 5614, from type host collected May 27, 1947 by Robert J. Newman at Cerro Conejo, San Luis Potosí, Mexico. Present status: *Sturnidoecus caligineus mexicanus* Carriker, 1956.

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Mitotic Activity in *Allium* After Treatment With Chromosome-Breaking Chemicals

BY

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ABSTRACT: A rapid method of mitotic evaluation was used to study the effect of chromosome altering chemicals upon mitotic activity. These chemicals were found to cause radical supression of mitosis in *Allium* meristematic cells.

It was suggested that since heterochromatin, the nucleic acid regulator, is damaged by these chemicals and nucleic acid quantitative changes effect mitotic rate that this might be the primary mechanism of inhibition of mitosis.

INTRODUCTION

Recently experiments have been performed to determine the action of radiomimetic chemicals on chromosomal aberrations. Ford (1948) found that nitrogen mustard caused more chromosomal anomalies in short chromosomes than in long ones. He observed that there were certain segments that seemed to have a greater frequency of these aberrations than others. Revell (1952) suggests that these "breaks" are possibly an interference of synthesis at certain points on the chromosome. He found in *Vicia faba* a great majority of the breaks were at the site of the heterochromatic segment of the L chromosome when these roots were treated with nitrogen mustard, diepoxide, and tertiary butyl hydroperoxide. X-rays gave a more random distribution of breaks. McLeish (1952) found that maleic hydrazide suppresses mitosis and causes breaks in chromosomes which have visible heterochromatin. Fahmy and Bird (1952) studied the effects of mustard gas, diepoxide, and triazine on the distribution of chromosome breaks of salivary gland cells of *Drosophila* and found two loci of considerable vulnerability. Both segments were heterochromatic in type. McLeish (1955) found that maleic hydrazide formed ascentric fragments, which carried nucleolar or-

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ganizers. Cells which contained 3,4, and 5 nucleolar organizers allowed fewer breakages than did normal cells with one or two nucleolar organizers. Smith and Lotfy (1955) observed the anaphase chromosomes of *Vicia* had aberrations in the heterochromatic regions that appeared to be effects during chromosomal duplication stages from treatment with propiolactone. However propiolactone caused the same frequency of chromosome breaks in *Allium* meristematic tissue, which lacks the visible heterochromatin. Oehlkers (1952) found that the greatest frequency of breaks was in the SAT-chromosome and within this chromosome the points of greatest susceptibility were the achromatic region separating the satellite from the rest of the chromosome and the centromere. Kihman (1956) showed that 8-ethoxycaffeine induced chromosome structural changes and caused a greater than random frequency of breaks in the attachment threads of satellites of *Allium cepa.*

It was believed of significance to find the effects of these chromosome breaking chemicals on mitosis. The procedure was made so as to give comparative results and not just an index of suppression or stimulation.

METHODS AND MATERIALS

Allium cepa bulbs of approximately similar sizes (3 cm. diameter) were placed, root primordia downward, in each of ten waxed paper drinking cups and ten milliliters of the solution to be tested was pipetted into them. A cardboard box was placed over the ten preparations and the bulbs were allowed to grow at room temperature. After 48 hours incubation five roots of comparable lengths were removed and placed in a single vial and treated with Feulgen stain using the method of Setterfield, Schreiber, and Woodard (1954). An ocular micrometer was used to obtain the distal two millimeters of the root which had been found to give a high percentage of meristematic cells. One thousand cells were individually observed from each bulb to give a total of ten thousand cells for each treatment that had been checked for mitotic activity.

1:2,3:4—diepoxybutane[1], caffeine[2], adenosine[2], adenine[2], adenylic acid[2], napthalene acetic acid[2], and benzidine[3] were made as 10^{-3}M water solutions. Methyl-bis(beta-chloroethyl) amine hydrochloride[4] was made as 5×10^{-4}M; tri-chlortriathylamin-chlorhydrat[5] as a 2×10^{-4}M; maleic hydrazide[2] as an 8×10^{-3}M; and the dimethyl benz(alpha) anthracene[3] was a saturated solution which gives a con-

1. Peninsular Chemresearch, Inc., Gainsville, Florida. 2. Nutritional Biochemical Co. 3. Eastman Organic Chemicals Distillation Products Industries, Rochester 3, N. Y. 4. Sharp and Dohme, West Point, Penn. 5. Nordmark-Werke GMBH-Hamburg, Germany.

centration of much less than 10^{-3}M. In preparing the nitrogen mustard solutions, chemical goggles, a mask dipped with a ten percent thiosulfate solution, hood with blower, and rubber gloves were utilized as precautionary measures.

A series of photographs was taken at 900X with the aid of an oil emmersion achromatic lens and Wratten filters G-15 and B-58.

RESULTS

Cells from roots grown in distilled water gave no apparent indication of anomalies as evidenced by the 293 mitotic figures which were found in the ten thousand cells observed. Nitrogen mustard, the bis form, on the other hand, caused many anomalies. Only twenty-six mitotic figures were seen of which almost fifty percent were classed as abnormal appearing. (See plate.) Examination of cells treated with diepoxybutane showed only seventeen were in mitosis and again over fifty percent of these mitotic figures were in an abnormal state. Maleic acid hydrazide was found to inhibit mitosis almost as much as the tris nitrogen mustard but these cells showed no anomalies.

Other substances were tried incidental to the problem. Napthalene acetic acid, a plant growth hormone, permitted growth in only three bulbs and the roots that did develop were thickened and short. However, the extent of the necrotic cells present in this preparation did not allow a percentage tabulation of mitotic figures. Several giant nuclei were seen (Fig. 1) in what appeared to be altered meristematic cells. They were approximately twenty times greater in area than normal nuclei as measured from enlarged photographs. The cortical cells were also hypertrophied. Purine derivatives were tried and all were found to be inhibitory. Only an occasional fragmented or undercharged chromosome was seen. Caffeine presented many abnormalities. Large nucleoli were observed, and cells which contained undercharged (weakly staining), irregularly dispersed anaphase chromosomes were present. Many pycknotic, karyorrhectic, and necrotic cells were found. In one hundred and eight mitotic figures present only eight were definitely believed to vary from the normal. Observation of the adenylic acid treated preparation was based upon only one thousand cells because the pectinase did not function properly in this case. Many binucleate cells were observed in the benzidine treated preparation and endopolyploidy was thought to have occurred in several instances. While only four abnormal mitotic figures were seen

the number of cells in prophase were unusually high. Treatment with dimethyl benz-anthracene produced relatively large nuclei in many of the cells along with many in which the cytoplasmic volume had also greatly increased. It was estimated that over fifty percent of the mitotic figures were in telophase in this preparation.

In a statistical analysis of the raw data an analysis of variance was used to ascertain the significant differences in the mean effects of the treatments. Bartlett's test for homogeneity of variance within each treatment showed significant differences at the 0.1% level. Treatment number six was left out of this test because of its obvious variability. After a square root transformation and a subsequent Bartlett's test, a value of 21 was obtained for Chi square with nine degrees of freedom, which is not significant at the 1% level. From the results (see table) it is seen that all treatments except number

TABLE 1.—Mitotic Activity (Each count expresses number of mitotic figures per thousand cells)

Chemical j^{th} treatment \ i^{th} plant		1	2	3	4	5	6	7	8	9	10	$\Sigma_i X_{ij}$
Control												
Distilled water	1	24	33	20	31	21	35	34	23	51	21	293
Heterochromatic breakers												
Nitrogen mustard (bis)	2	1	16	2	3	1	0	1	0	1	1	26
Diepoxybutane	3	2	3	0	3	1	1	2	2	2	1	17
Nitrogen mustard (tris)	4	6	9	2	3	16	7	2	4	6	4	59
Maleic hydrazide	5	2	12	5	10	4	6	5	0	5	4	53
Carcinogens												
Bendzidine	6	0	53	0	5	1	33	36	56	13	53	250
Dimethyl-benz anthracene	7	16	0	0	7	13	1	26	0	3	9	75
Purine derivatives												
Adenine	8	23	30	47	17	26	38	19	15	45	21	286
Adenosine	9	13	21	30	7	13	15	13	22	19	28	181
Adenylic acid	10	10	20	20	30	0	0	0	20	10	0	110
Caffeine	11	16	29	9	14	7	5	8	5	12	3	108

three have wide variability. When an analysis of variance is computed for the group (1, 2, 3, 4, 5, 7, 8, 9, 10, 11), there is shown a significant difference between treatments, ($F_{9,90} = 14.98$; $P < .01$). The same test when applied to treatments 2, 3, 4, and 5 as a group (the heterochromatic breakers) gave a significant difference between treatments of this group, ($F_{3,36} = 42.19$; $P < .01$). Also 8, 9, and 10 show wide variation, ($F_{2,27} = 73.125$; $P < .01$).

DISCUSSION

The results (see table) show that chemicals which act on heterochromatin in other cells depress mitotic activity considerably in *Allium cepa* cells. Diepoxybutane caused the greatest reduction of mitosis and is also the most consistent in the breaking of heterochromatin of the chemicals used (Revell 1952). The bis form of nitrogen mustard was more active as a depressant to mitosis than the tris form. Maleic hydrazide and tris nitrogen mustard gave similar results.

Benzidine acted very peculiarly. It depressed mitosis drastically in four bulbs yet may have had a stimulating effect on others. The purine derivatives show depression as a gradient of their molecular weight with adenine giving almost no effect. The plant growth hormones were found to depress the cell division of the predominantly meristematic tissue samples, since they act primarily as a stimulus to differentiated cortical cells and not to meristematic cells.

A major consideration is the correlation between chromosome aberrations and their influence on the role of mitosis. Nitrogen mustard can effect heterochromatin (Revell '52). Heterochromatin, in turn, controls the nucleic acid supply of the cell. (Schultz 1947, Caspersson 1950). Rate of division can be explained by assuming a quantitative change in nucleic acid synthesis (Koller 1951). This then could be a mechanism for the necessary correlations between chromosome altering chemicals such as those used in this work and the suppressed mitotic effect. This mechanism could be termed "heterochromatic suppression."

SUMMARY

A recently developed rapid method of mitotic evaluation using pectinase was used to study the effect of groups of chemicals, which effect cell systems, upon mitotic activity. Chemicals that previously have been shown to disrupt heterochromatic segments were found to depress mitotic activity extensively. A possible mechanism of action is suggested. Purine derivatives, a plant hormone, and carcinogens were also evaluated for their effects on mitotic activity.

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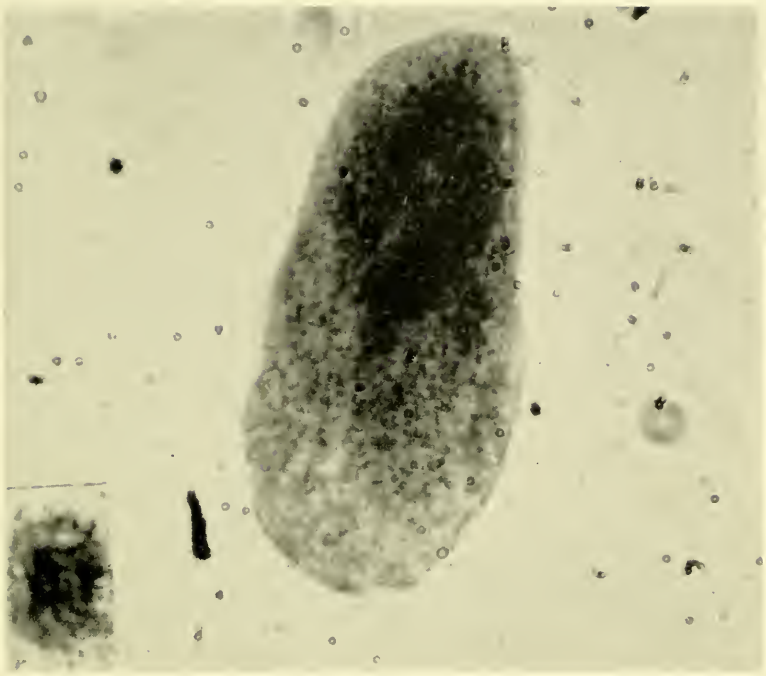

FIG. 1. A giant nucleus in a cell treated with napthalene acetic acid. Feulgen stain. Inset shows normal size of nucleus. (Enlarged from 900 ×.)

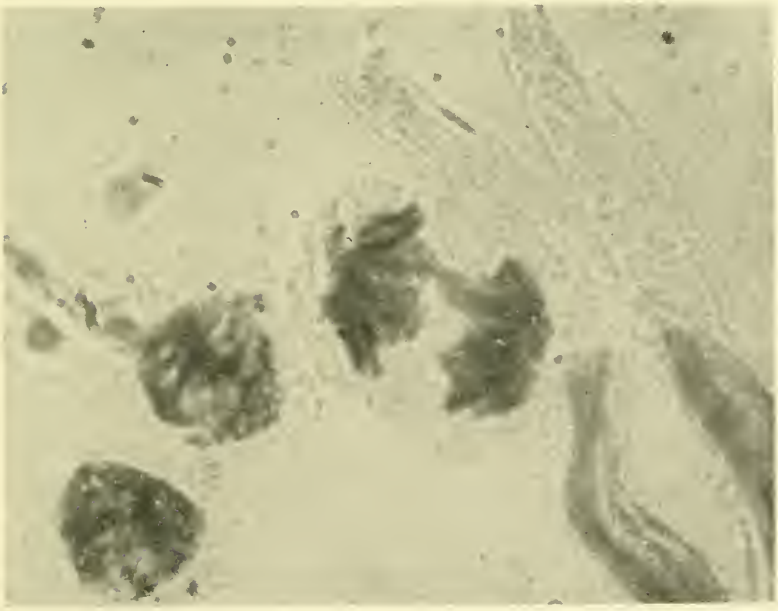

FIG. 2. A criss cross anaphase bridge in a cell treated with nitrogen mustard. Feulgen stain. (Enlarged from 900 ×.)

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